Plant functional group diversity as a mechanism for invasion resistance
by Monica Lynn Pokorny

A thesis submitted in partial fulfillment of the requirements for the degree of Masters of Science in
Land Resources and Environmental Sciences
Montana State University
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Abstract:

The current rate of nonindigenous plant invasion has important ramifications to indigenous ecosystems. A proposed mechanism for invasion resistance is that diverse plant assemblages enhance niche occupation and preempt resources otherwise available to invaders. Unfortunately, research on diversity as a mechanism for resistance has confounding results. The purpose of this study was to quantify species and functional group diversity in a grassland plant community in Montana, investigate the ability of plant functional groups to resist invasion by a nonindigenous species, and to quantify and compare portions of the nutrient and hydrologic cycles of the following indigenous functional groups; grasses, shallow-rooted forbs, deep-rooted forbs, spikemoss, and the nonindigenous invader, *Centaurea maculosa*. The study consisted of a factorial combination of seven functional group removals (groups singularly or in combination) and two *C. maculosa* treatments (seeded vs. absent) applied in a randomized-complete-block design replicated four times at two sites. Diversity by functional group was recorded in 2000. I documented a higher diversity than has previously been described for the *Festuca idahoensis*/*Agropyron spicatum* habitat type and found forbs represented the majority of the richness and biomass of the grassland community. *Centaurea maculosa* density was counted in 2001 and analyzed using ANOVA. *Centaurea maculosa* density depended upon the functional groups removed. The highest *C. maculosa* densities occurred where all vegetation (50 plants m²) or all forbs (18 plants m²) were removed from plots. *Centaurea maculosa* densities were the lowest (2-7 plants m²) in plots where nothing, shallow-rooted forbs, deep-rooted forbs, grass, or spikemoss were removed. Functional group biomass was collected and analyzed for N, P, K, and S. ANOVA indicated percent tissue concentration and nutrient uptake differed among functional groups. *Centaurea maculosa* tissue nutrient percent was most similar to shallow-rooted forbs. Similarly, indigenous forb functional groups were most similar in nutrient uptake levels to *C. maculosa*. This study suggests forbs are an important component to grassland community diversity, and establishing and maintaining a diversity of plant functional groups within the community enhances resistance to invasion. Indigenous forbs were particularly important to resisting invasion by nonindigenous forbs. Since indigenous forbs were functionally similar in percent tissue concentration and plant nutrient uptake to the nonindigenous forb, they may be increasing resource competition with *C. maculosa* and decreasing invasion success. Functional group diversity and forb diversity should be a larger consideration in invasive plant management.

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ABSTRACT

The current rate of nonindigenous plant invasion has important ramifications to indigenous ecosystems. A proposed mechanism for invasion resistance is that diverse plant assemblages enhance niche occupation and preempt resources otherwise available to invaders. Unfortunately, research on diversity as a mechanism for resistance has confounding results. The purpose of this study was to quantify species and functional group diversity in a grassland plant community in Montana, investigate the ability of plant functional groups to resist invasion by a nonindigenous species, and to quantify and compare portions of the nutrient and hydrologic cycles of the following indigenous functional groups; grasses, shallow-rooted forbs, deep-rooted forbs, spikemoss, and the nonindigenous invader, *Centaurea maculosa*. The study consisted of a factorial combination of seven functional group removals (groups singularly or in combination) and two *C. maculosa* treatments (seeded vs. absent) applied in a randomized-complete-block design replicated four times at two sites. Diversity by functional group was recorded in 2000. I documented a higher diversity than has previously been described for the *Festuca idahoensis*/*Agropyron spicatum* habitat type and found forbs represented the majority of the richness and biomass of the grassland community. *Centaurea maculosa* density was counted in 2001 and analyzed using ANOVA. *Centaurea maculosa* density depended upon the functional groups removed. The highest *C. maculosa* densities occurred where all vegetation (50 plants m^{-2}) or all forbs (18 plants m^{-2}) were removed from plots. *Centaurea maculosa* densities were the lowest ($2\text{-}7 \text{ plants m}^{-2}$) in plots where nothing, shallow-rooted forbs, deep-rooted forbs, grass, or spikemoss were removed. Functional group biomass was collected and analyzed for N, P, K, and S. ANOVA indicated percent tissue concentration and nutrient uptake differed among functional groups. *Centaurea maculosa* tissue nutrient percent was most similar to shallow-rooted forbs. Similarly, indigenous forb functional groups were most similar in nutrient uptake levels to *C. maculosa*. This study suggests forbs are an important component to grassland community diversity, and establishing and maintaining a diversity of plant functional groups within the community enhances resistance to invasion. Indigenous forbs were particularly important to resisting invasion by nonindigenous forbs. Since indigenous forbs were functionally similar in percent tissue concentration and plant nutrient uptake to the nonindigenous forb, they may be increasing resource competition with *C. maculosa* and decreasing invasion success. Functional group diversity and forb diversity should be a larger consideration in invasive plant management.

CHAPTER 1

INTRODUCTION

Nonindigenous plants have invaded and now dominate millions of hectares of grasslands throughout western North America (Sheley and Petroff 1999). The current rate of nonindigenous plant invasion is an anthropogenic process with important ramifications to our native ecosystems (Rejmanek 1996, Vitousek et al. 1997).

Nonindigenous plants may be permanently altering the structure and function of indigenous ecosystems (Mack and D'Antonio 1998, Olson 1999). Research implies invasive plant species can degrade soil and water resources (Lacey et al. 1989), reduces wildlife and livestock habitat and forage (Hakim 1979), and alter community structure by decreasing the density, biomass, and basal area associated with indigenous plant communities (Olson 1999, Christain and Wilson 1999, Kedzie-Webb et al. 2001).

Most current invasive plant strategies are technology or tool based and rarely meet long-term management objectives. Successful invasive plant management will require a shift from that of invasive plant control to developing and maintaining plant communities that function at a sustainable level and resist invasion. Invasive plant management must be based on the principles and concepts directing plant community dynamics (Sheley et al. 1996). These principles must be founded in ecology, the basic science behind land management, and must focus on establishing and/or maintaining desired plant communities, rather than simply controlling unwanted plants. An objective of sustainable invasive plant management will be to develop plant communities that are relatively weed-

resistant, while meeting other land use objectives, such as forage production, wildlife habitat development, or recreational land maintenance (Sheley et al. 1996).

Susceptibility of western North America grasslands to invasion may be influenced by community structure and/or resource availability (Elton 1958, Burke and Grime 1996, Stoltgren et al. 1999). The composition of North American grasslands has been described in plant community classifications. The focus of these classifications has been on managing grasses for livestock production and less attention has been given to other vegetative life-form's diversity, composition, and response to management (Daubenmire 1970, Mueggler and Stewart 1980). If plant community structure can effect the invasibility of a plant community, a more thorough description is needed of indigenous species and functional group diversity throughout a growing season in western North American grasslands. This may require a change from traditional field sampling techniques. Plant community structure may also be mechanistically linked to invasion through resource availability. One of the most commonly cited mechanisms for invasion resistance is that diverse plant assemblages use resources more completely (Levine and D'Antonio 1999, Tilman 1997). Thus increased indigenous functional diversity preempts available resources (Dukes 2001, Davis and Pelsor 2001) and decreases invader recruitment (Robinson et al. 1995). Research clarifying resource-based invasion mechanisms is needed because support of these hypotheses is confounding and incomplete. The potential for a particular functional group, or combination of functional groups, to resist invasion could have important implications for invasive plant management.

If the goal of sustainable invasive plant management is to direct plant communities to a desired state, then ecologists and land managers need an understanding of the ecological role of indigenous and nonindigenous functional groups. To date, little is known about the ecological role of indigenous species, or functional groups of species, and nonindigenous invaders occurring within grasslands. Furthermore, little is known about plant function and ecosystem processes as functional group diversity changes. Altering plant functional group diversity and composition may influence the nutrient and water cycling within the plant community and affect its invasibility (Hooper and Vitousek 1997, Tilman 1997, Dukes 2001). Understanding the ecological role of indigenous and nonindigenous functional groups is important because it provides basic information about plant community dynamics and ecological impacts of invaders. It also provides baseline information necessary for developing restoration goals, assessing the effects of management, and directing plant communities to a desired state (Pickett et al. 1987, McLendon and Redente 1991, Sheley et al. 1996). Therefore, understanding the ecological role of various functional groups would provide a basis for designing and maintaining weed-resistant plant communities.

This research investigates ecological principles related to invasive plant management. The study had three specific objectives and several hypotheses:

- I. To quantify the functional diversity of a grassland ecosystem. Specific objectives were to measure the richness and density of functional groups within the grassland community, measure the biomass of each functional group, and calculate diversity indices for each functional group. I hypothesized that the species and functional group diversity would be

greater than previous descriptions of the *Festuca idahoensis*/*Agropyron spicatum* habitat type of a given location because of my multiple-visits method of describing the community. Of the species present, I hypothesized that forb functional groups account for the majority of the richness and biomass of a grassland plant community.

II. To investigate the ability of functional groups (singularly or in combination) to resist invasion by a nonindigenous species, *Centaurea maculosa* (spotted knapweed). I

hypothesized that removing a functional group would yield higher *C. maculosa* densities and biomass than the control, and that *C. maculosa* density and biomass would increase as functional groups were progressively removed. I also hypothesized that removing forb functional groups would increase *C. maculosa* biomass and density more than removing grasses because indigenous and nonindigenous forbs may share physiological and morphological traits and ecosystem function.

III. To quantify the ecological role of indigenous functional groups and a nonindigenous invader. My specific objectives were to quantify portions of the nitrogen (N), phosphorus (P), potassium (K), sulfur (S), carbon (C), and water cycles of the following indigenous functional groups: shallow-rooted forbs, deep-rooted forbs, grasses, spikemoss, and a nonindigenous invader, *Centaurea maculosa*. I hypothesized that indigenous functional groups have different ecological roles, and that removing a functional group would alter the soil nutrient and hydrologic cycles, with the impact increasing with removal intensity. I also hypothesized indigenous and nonindigenous forbs would have similar ecological roles cycling N, P, K, S, and C in plant tissue because they share morphological and physiological traits. Because nonindigenous invaders are thought to impact ecosystem

processes, I hypothesized *C. maculosa* would alter soil nutrient and water cycles, and that the presence of *C. maculosa* would alter an indigenous functional groups ability to capture resources.

Specific objectives and hypotheses are addressed separately in Chapters 2, 3, and 4. A general review of the results of this study are presented in Chapter 5.

References

- Burke, M. J., and J.P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* 77(3): 776-790.
- Christian, J. M., and S.D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the northern great plains. *Ecology* 80(7): 2397-2407.
- Daubenmire, R. 1970. *Steppe Vegetation of Washington*. Washington State University Cooperative Extension, Pullman, Washington.
- Davis, M.A., and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. *Ecology Letters* 4: 421-428.
- Dukes, J. 2001. Biodiversity and invasibility in grassland microcosms. *Oecologia*. 126: 563-568.
- Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. The University of Chicago Press, Chicago, Illinois.
- Hakim, S. E. A. 1979. Range condition of the Threemile game range in western Montana. Thesis (M. S.) University of Montana, Missoula, Montana.
- Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Nature* 277: 1302-1305.
- Kedzie-Webb, S. A., R.L. Sheley, J.J. Borkowski, and J.S. Jacobs. 2001. Relationships between *Centaurea maculosa* and indigenous plant assemblages. *Western North American Naturalist*. 61(1): 43-49.
- Lacey, R. L., C. B. Marlow, and J. R. Lane. 1989. Influence of spotted knapweed (*Centaurea maculosa*) on surface runoff and sediment yield. *Weed Technology* 3: 627-631.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of the evidence linking diversity and invasibility. *Oikos* 87: 15-26.
- Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13(5): 195-198.
- McLendon, T., and E. F. Redente. 1991. Nitrogen and phosphorus effects on secondary succession dynamics on a semi-arid sagebrush site. *Ecology* 72(6): 2016-2024.

- Mueggler, W. F., and W. L. Stewart. 1980. Grassland and Shrubland Habitat Types of Western Montana. Intermountain Forest and Range Experimental Station, Ogden, Utah.
- Olson, B. E. 1999. Impacts of noxious weeds on ecological and economic systems. *In* The Biology and Management of Noxious Rangeland Weeds. R. L. Sheley and J. K. Petroff (eds.), pp. 4-18. Oregon State University Press, Corvallis, Oregon.
- Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms and pathways of succession. *The Botanical Review*. 53(3): 335-371.
- Rejmanek, M. 1996. A theory of seed plant invasiveness: the first sketch. *Biological Conservation* 78: 171-181.
- Robinson, G. R., J. F. Quinn, and M. L. Stanton. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* 76(3): 786-794.
- Sheley, R. L., and J. K. Petroff (eds.). 1999. The Biology and Management of Noxious Rangeland Weeds. Oregon State University Press, Corvallis, Oregon.
- Sheley, R. L., T. J. Svejcar, and B.D. Maxwell. 1996. A theoretical framework for developing successional weed management strategies on rangeland. *Weed Technology* 10: 766-773.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* 69(1): 25-46.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78(1): 81-92.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, J. M. Melillo. 1997. Human domination of earth's ecosystems. *Science* 277: 494-499.

CHAPTER 2

DIVERSITY OF FUNCTIONAL GROUPS IN A GRASSLAND PLANT
COMMUNITY: EVIDENCE FOR FORBS AS A CRITICAL
MANAGEMENT CONSIDERATIONIntroduction

Grasslands are the largest vegetative form on earth, comprising 24% of the world's vegetation, and about 125 M hectares of the United States (Sims and Risser 2000). Near the start of the 20th century, descriptions of grasslands focused on understanding the value of species for livestock grazing, and little quantitative data was used to describe plant community productivity or species composition and function in the system (Kearney et al. 1914, Shantz and Piemeisel 1924). Grasslands soon began to be described by their particular climax plant community. Clements (1920) classified and described the grasslands of the western United States as one of five grassland formations. Since Clements, ecologists have recognized and described finer level classifications of the grasslands. Stoddart and Smith (1943) described 18 range types, based on presence and abundance of characteristic plant species. More recent classifications of grassland habitat types in the northwestern United States identified major grassland vegetation types, seral stages of each type, and response to grazing management practices (Daubenmire 1970, Mueggler and Stewart 1980). A common trend of these classification systems is the vegetative type's grass species nomenclature and the emphasis on managing grass for

livestock production (Stoddart and Smith 1943, Daubenmire 1970, Mueggler and Stewart 1980, Willoughby et al. 1998).

While forbs species are listed as diverse components of grassland communities (Daubenmire 1970, Sims et al. 1978, Jensen et al. 1988b, Mueggler and Stewart 1980, Hogg et al. 2001), they have not been a primary focus in classification and land management practices (Willoughby et al. 1998, Fuhlendorf and Engle 2001), perhaps because forb species composition varies with environmental and biological factors (MacCracken et al. 1983), or because forbs have the greatest production variability within habitat types (Jensen et al. 1988a). Conversely, year-to-year and site-to-site variation of forbs may be a function of methodology limitations in these classifications. Vegetative classifications have historically documented species composition only once during the growing season (Stoddart and Smith 1943, Daubenmire 1970, Mueggler and Stewart 1980, Jensen et al. 1988b). Depending on annual variation in climate, early or late developing forbs may have been missed in data collection for classification descriptions. Measuring diversity once, at peak standing crop, does not account for the diversity of spring or fall forbs. To estimate the actual community diversity and the diversity of forbs within a site, periodic field sampling must occur.

Ecologists and land managers have recognized the importance of diverse plant communities in maintaining healthy ecosystems (Darwin 1859, Elton 1958, MacArthur and Wilson 1967, Goodman 1975, Pimm 1991). It is possible that forbs, or groups of forbs with similar characteristics, are important management groups and play a vital role in ecosystem functions such as invasion resistance and nutrient cycling (Symstad 2000,

Dukes 2001, Tilman et al. 2001). We investigated the ecological role of indigenous groups of forbs in companion papers (Chapters 3 and 4) to further develop the concept of forb diversity as a critical management group. In spite of the potential role of forbs in plant community processes, only limited attention is given to their composition in grasslands during management practices. The role of various components, particularly forbs, need to be considered more seriously in future grassland management.

The purpose of this research was to quantify species and functional group diversity in a grassland plant community in southwestern Montana. Our first specific objective was to identify the plant species in the grassland and separate the species into functional groups, based on their morphology and physiology, to provide important management units. Other specific objectives were to measure the richness and density of functional groups within the grassland community, measure the biomass of each functional group, and calculate diversity indices for each functional group. Additionally, we classified the soils and quantified site and season soil nutrient levels. We hypothesized that the species and functional group richness would be greater than previous descriptions of the habitat type of a given location because of our multiple-visits method of quantifying the community. Of the species present, we hypothesized that forb functional groups account for the majority of the richness and biomass of a grassland plant community.

Methods

Study sites

This study was conducted on two sites within the *Festuca idahoensis*/*Agropyron spicatum* habitat type (Mueggler and Stewart 1980). This habitat type lies at the cool-wet end of grassland habitat types and can be found at elevations ranging from 1,400 to 2,300 meters. Predominant indigenous perennial grasses include Idaho fescue (*Festuca idahoensis* Elmer) and bluebunch wheatgrass (*Agropyron spicatum* Pursh). The proportion of forbs to graminoids varies with location for this habitat type (Mueggler and Stewart 1980). Some predominant indigenous forbs in the system include prairie sage (*Artemisia ludoviciana* L.), arrowleaf balsamroot (*Balsamorhiza sagittata* [Pursh] Nutt), and lupine (*Lupinus* spp.). Medium shrubs are absent from this habitat type unless it has been severely disturbed. We chose the Idaho fescue/bluebunch wheatgrass habitat type because it is widely distributed throughout the mountain grasslands in southwestern Montana and the western United States and provides a model system for applied ecological research.

Sites were located on the Flying D Ranch approximately 70 km east ($45^{\circ}34' \text{ N}$, $111^{\circ}34' \text{ W}$) of Bozeman, Montana. Sites lie on an east-northeast aspect of a 20 degree slope at 1,624 m elevation. Our specific sites were chosen because they were near enough to one another to be considered similar, but appeared to represent different seral stages within the Idaho fescue/bluebunch wheatgrass habitat type. Prior to plot establishment, soils were tested for the presence of picloram (4-amino-3,5,6-trichloropicolinic acid,

potassium salt) to minimize the risk that site characteristics and plant community composition were influenced by recent herbicide applications. Picloram was not detected at the 0.01 mg/kg level. Soils were classified in August, 2000. Annual average precipitation is 41 cm and annual average temperature ranges from 5.5 to 7°C.

The area has been grazed for decades, and in some years it has been heavily grazed, by either cattle or bison (*Bison bison*) in its recent history (50-60 years). Bison grazing during the past ten years has been sporadic. Windblown slopes are prime winter habitat for wildlife. In the study area, winter use by elk (*Cervus elaphus*) has steadily increased as herd size increased during the past 20 years.

Experimental design and sampling

This study was a portion of a larger research project that involved removing functional groups of plants. Therefore, the design of this research was aimed at achieving multiple objectives. Species of grass, forbs and spikemoss were combined into functional groups based on morphological and physiological similarities. Grasses, forbs, and spikemoss were split into functional groups. Forbs were further divided into two functional groups based on average rooting depth of each species, determined by careful excavation of each species to determine root structure and rooting depth. The distinction between a shallow and a deep depth was based on a natural break within the roots sampled which occurred at about 15 cm. In cases where the average root depth was close to 15 cm, species with primarily fibrous roots were considered shallow-rooted, while tap-roots were grouped with deep-rooted forbs.

Removal treatments were arranged in a randomized-complete-block design with four replications on each of two sites. Treatments were applied by removing a functional group or groups in combination from the 2 x 2 meters plots. This study consisted of seven removal treatments 1) shallow-rooted forb, 2) deep-rooted forb, 3) all forbs, 4) grasses, 5) all plant material, 6) nothing (control) and 7) moss, lichens and spikemoss (collectively referred to as spikemoss throughout the paper) removed. While removing functional groups in 2000, species richness and density were recorded for all species removed, as well as all species on the control plots (nothing removed). Species richness was measured by counting all species present on the plot. Forb density was measured by counting the number of plants per species in the plot. Grass density was determined by counting the number of tillers per species within a 0.2 x 0.5 m frame. A single frame was placed randomly in each plot. Plant removal and data recording, continued every-other week throughout the 2000 growing season to capture seasonal variation of plant composition. For the spikemoss functional group, percent foliar cover was estimated within a 0.2 x 0.5 m frame for each species representing one percent or greater of the plot area. Forbs and *Selaginella* species were identified using Dorn (1984) while grasses follow the nomenclature in Cronquist et al. (1977). Mosses and lichens were identified using Flowers (1973) and McCune (1995).

Aboveground biomass of the shallow-rooted forbs, deep-rooted forbs and grasses was collected during the spring, summer, and fall of 2001 from all plots where their biomass was not removed as a treatment. Thus, there are different sample sizes for each group. Spring sampling occurred when the majority of the spring ephemeral forbs were in

bloom, summer sampling coincided with peak standing crop, and fall sampling occurred after 95% of the vegetation was senescent. Plots were divided into three subplots which were randomly assigned to each of the three sample periods to prevent sampling the same area twice. Plants were clipped to ground level within three 0.2 x 0.5 m frames randomly placed in each subplot. Plant aboveground biomass was separated by functional group as it was clipped. As part of the treatments, spikemoss was removed from 2 plots in each block. Plant tissues were oven dried (40° C, 160 hours) to a constant weight, weighed, and biomass was recorded.

Soils samples were collected from each control plot with a 2.2 cm diameter soil core during the spring, summer, and fall of 2001 to measure nutrient concentrations of each sites. Within each subplot, randomly located soil cores were collected. The soil cores were divided into two depths (0-15 cm and 15-40 cm) to coincide with the depths of shallow-rooted and deep-rooted forb functional groups. To capture heterogeneity of soil properties at each season, three samples per depth were collected from each plot and were combined into one sample per plot for analysis. These soils were analyzed for mass water content, total nitrogen (N), nitrate ($\text{NO}_3\text{-N}$), ammonium ($\text{NH}_4\text{-N}$), sulfur (S), phosphorus (P), potassium (K), and total carbon (C) at each site. Soil samples collected from the field were weighed wet, dried in a forced-air oven (40° C, 160 hours) to a constant weight, and weighed again to determine mass water content (Brady and Weil 1999). Soil samples were then ground to pass through a 2 mm sieve in preparation for chemical analyses. Inorganic soil N ($\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$) was determined on 1 M KCl extracts of soils (5 g soil:50 ml extractant) (Mulvaney 1996) and total N was determine using the Kjeldahl

(TKN) method (Bremner 1996). Available P in the soil was measured by the NaHCO_3 extraction method (Olsen et al., 1954). Available K and S were determined by extraction with 1 M NH_4OAC (Helmke and Sparks, 1996) and 0.001 M CaCl_2 (Hamm et al., 1973), respectively, using a 5:1 extractant to soil ratio. Filtered extracts were analyzed for P, K, and S by inductively coupled plasma membrane spectroscopy (Jones, 1977). Total C was determined by loss-on-ignition (Nelson and Sommers 1996).

Data analysis

Plant. Species frequency of occurrence was calculated for each site to determine species distribution between the sites. Richness, biomass, and density were summarized for the shallow-rooted forb, deep-rooted forb, and grass functional groups individually and for the total plot. Biomass was averaged over the three seasons. For the spikemoss functional group, mean percent cover, richness, and biomass were summarized. Richness was always summarized per plot (4 m^2) while density, biomass, and percent cover were averaged per meter square. Both the Simpson and Shannon-Weaver diversity indexes were calculated for each functional group. The Simpson Diversity Index is defined as $D = 1/(\sum(P_i^2))$ where P_i is the proportion of the i^{th} species (Begon et al. 1990). The Shannon-Weaver Index is defined as $H = -\sum(P_i(\ln P_i))$ (Begon et al. 1990). Data comparisons were conducted using the Student's t -test in SPSS software (SPSS version 10.0 1999).

Soil. Mean mass water content and nutrient levels were determined for each site, season, and soil depth. C:N ratio was calculated for each site and depth. Soils were

analyzed for site differences in water and nutrient content at each soil depth using a Student's *t*-test. We used the combined means of seasons for nutrients and water site comparisons. A one-way ANOVA was used to analyze mass water content and nutrient level variations among seasons at each soil depth and site. At site 2, the deep soil depth phosphorus did not meet the assumptions of equality of variance and normality and data transformations did not improve the model. Therefore, the Mann-Whitney non-parametric test was used. We used SPSS software for the above analyses. Test results were considered significant at the $\alpha = 0.05$ level.

Results

Frequency, density, biomass, and cover

All functional groups and twenty-four plant families were represented on the study sites. The plant families most often encountered were Asteraceae (16 taxa), Fabaceae (7 taxa), and Poaceae (14 taxa). In total, 90 vegetative species were identified in this grassland system (Table 2.1). Of those species, 47 were shallow-rooted forbs, 22 were deep-rooted forbs, 14 were grasses, 4 were lichens, 1 was a spikemoss, and 2 were mosses. Shallow-rooted forbs (0-15 cm roots) consisted of annual, short-lived perennial, and perennial species with bulbs, rhizomes, fibrous roots and/or shallow tap-roots. Deep-rooted forbs (15-40+ cm roots) were primarily perennial tap-rooted plants with varying lateral root lengths and depths. Idaho fescue and bluebunch wheatgrass were the most commonly occurring grasses. Arrowleaf balsamroot, lupine, prairie milkvetch (*Astragalus adsurgens* Pallas), and blazing star (*Liatris punctata* Hook) are deep-rooted forbs which

Table 2.1. Species functional group assignment, average root depth, and frequency on site 1 and site 2, respectively.

Species	Common Name	Functional	Average Root	Frequency of
		Group	Depth (cm)	occurrence
<i>Achillea millefolium</i> L.	Yarrow	S	10	0.28 / 0.21
<i>Allium cernuum</i> Roth.	Nodding onion	S	5	0.97 / 1.00
<i>Alyssum alyssoides</i> L.	Alyssum	S	3	0.06 / 0.00
<i>Antennaria parvifolia</i> Nutt.	Small leaf pussytoes	S	11	0.65 / 0.66
<i>Arabis nuttallii</i> Robinson	Nuttall Rockcress	S	5	1.00 / 0.34
<i>Arenaria congesta</i> Nutt.	Ballhead sandwort	S	4	0.97 / 1.00
<i>Arnica sororia</i> Greene	Arnica	S	10	0.28 / 0.25
<i>Artemisia campestris</i> L.	Common sagewort	S	12	0.09 / 0.00
<i>Artemisia dracunculus</i> L.	Green sagewort	S	3	0.06 / 0.00
<i>Artemisia frigida</i> Willd.	Fringed sage	S	14	1.00 / 0.40
<i>Artemisia ludoviciana</i> L.	Man sage	S	3	0.31 / 0.28
<i>Astragalus agrestis</i> Dougl. Ex Hook	Field milkvetch	S	10	0.00 / 0.09
<i>Besseyia wyomingensis</i> (A. Nels.) Rydb.	Kittentail	S	12	0.97 / 0.91
<i>Castilleja pallescens</i> (Gray) Greene	Pale Indian paintbrush	S	7	1.00 / 1.00
<i>Cerastium arvense</i> L.	Chickweed	S	8	1.00 / 0.94
<i>Chenopodium leptophyllum</i> Nutt.	Lambsquarter	S	7	0.09 / 0.03
<i>Comandra umbellata</i> (L.) Nutt.	Bastard Toadflax	S	4	1.00 / 0.90
<i>Dodecatheon conjugens</i> Greene	Shooting star	S	6	0.97 / 0.90
<i>Douglasia montana</i> Gray	Mountain Douglasia	S	9	1.00 / 0.88
<i>Erigeron caespitosus</i> Nutt.	Tufted Fleabane	S	13	0.90 / 0.90
<i>Erysimum asperum</i> Nutt DC.	Plains Wallflower	S	5	0.16 / 0.00
<i>Erysimum inconspicuum</i> (Wats.) MacM.	Wallflower	S	6	0.09 / 0.00
<i>Fritillaria pudica</i> Pursh	Yellow bell	S	6	0.97 / 1.00
<i>Gaillardia aristata</i> Pursh	Blanketflower	S	6	1.00 / 1.00
<i>Galium boreale</i> L.	Bedstraw	S	3	0.22 / 0.00
<i>Gaura coccinea</i> Nutt. Ex Pursh	Gaura	S	3	0.09 / 0.03
<i>Gutierrezia sarothrae</i> Britt. & Rusby	Broom snakeweed	S	6	0.63 / 0.72
<i>Haplopappus acaulis</i> Nutt.	Goldenweed	S	7	0.00 / 0.03
<i>Heterotheca villosa</i> Pursh	Golden aster	S	6	0.59 / 0.75
<i>Iris missouriensis</i> Nutt.	Bearded Iris	S	11	0.90 / 0.00

(Table 2.1 continued)

Species	Common Name	Functional	Average Root	Frequency of
		Group	Depth (cm)	occurrence
<i>Linum lewisii</i> Pursh	Flax	S	8	0.97 / 1.00
<i>Lesquerella alpina</i> (Nutt.) Wats.	Alkaline bladderpod	S	7	0.19 / 0.00
<i>Lomatium cous</i> Coult. & Rose	Mountain Lomatium	S	12	0.94 / 0.75
<i>Musineon divaricatum</i> Pursh	Musineon	S	10	0.13 / 0.06
<i>Nothocalais cuspidata</i> (Pursh) Greene	Cuspidate nothocalais	S	14	1.00 / 1.00
<i>Nothocalais troximoides</i> (Gray) Greene	Nothocalais	S	8	0.56 / 0.97
<i>Penstemon eriantherus</i> Pursh	Penstemon	S	4	1.00 / 1.00
<i>Sedum borschii</i> Clausen	Stone crop	S	3	0.03 / 0.00
<i>Senecio canus</i> Hook	Woolly groundsel	S	8	0.94 / 0.66
<i>Sisyrinchium montanum</i> Greene	Blue eye grass	S	5	0.97 / 0.72
<i>Vicia americana</i> Muhl. Ex Willd.	American vetch	S	10	0.97 / 0.88
<i>Viola nuttallii</i> Pursh	Yellow violet	S	4	0.72 / 0.84
<i>Viola nuttallii</i> var. <i>vallicola</i> A. Nels.	Yellow violet	S	4	0.03 / 0.03
<i>Zigadenus venenosus</i> Wats.	Death camas	S	6	1.00 / 1.00
Unknown forb 1	Unknown forb	S	5	0.03 / 0.00
Unknown forb 2	Unknown forb	S	6	0.03 / 0.00
Unknown forb 3	Unknown forb	S	3	0.03 / 0.00
<i>Anemone multifida</i> Poir.	Ball anemone	D	19	0.06 / 0.00
<i>Anemone patens</i> L.	Pasque flower	D	26	0.50 / 0.97
<i>Astragalus adsurgens</i> Pallas	Prairie milkvetch	D	30	1.00 / 0.94
<i>Astragalus crassicaulus</i> Nutt.	Plum milkvetch	D	20	0.41 / 0.84
<i>Balsamorhiza sagittata</i> (Pursh) Nutt	Arrowleaf Balsamroot	D	35	1.00 / 0.78
<i>Clematis hirsutissima</i> Pursh	Vase flower	D	24	0.25 / 0.03
<i>Crepis acuminata</i> Nutt.	hawkbeard	D	16	0.19 / 0.06
<i>Crepis occidentalis</i> Nutt.	hawkbeard	D	20	0.59 / 0.66
<i>Frasera speciosa</i> Dougl. ex Griseb	Green gentian	D	30	0.56 / 0.84
<i>Geum triflorum</i> Pursh	Prairie smoke	D	19	0.13 / 0.06
<i>Geranium viscosissimum</i> Fisch	Sticky geranium	D	20	0.00 / 0.03
<i>Heuchera parviflora</i> Nutt.	Littleleaf allumroot	D	20	0.44 / 0.00
<i>Ipomopsis spicata</i> Nutt. (Grant)	Spike Ipomopsis	D	27	0.56 / 0.88

(Table 2.1 continued)

Species	Common Name	Functional	Average Root	Frequency of
		Group	Depth (cm)	occurrence
<i>Liatris punctata</i> Hook	Blazing star	D	19	1.00 / 0.97
<i>Lithospermum ruderae</i> Dougl.ex. Lehm	Puccoon	D	35	0.63 / 0.84
<i>Lupinus sericeus</i> Pursh	Lupine	D	35	0.97 / 0.97
<i>Mertensia oblongifolia</i> (Nutt.) G. Don	Bluebell	D	20	0.09 / 0.00
<i>Phlox albomarginata</i> Jones	Phlox	D	16	0.41 / 0.66
<i>Oxytropis lagopus</i> Nutt.	Haresfoot loco	D	20	0.06 / 0.13
<i>Oxytropis sericea</i> Nutt.	White Pointloco	D	20	0.50 / 0.81
<i>Taraxacum officinale</i> Weber	Common Dandelion	D	18	0.97 / 1.00
<i>Tragopogon dubius</i> Scop.	Goatsbeard	D	18	0.41 / 0.69
<i>Agropyron spicatum</i> Pursh	Bluebunch wheatgrass	G	15	1.00 / 0.96
<i>Aristida longiseta</i> L.	Red three-awn	G	15	0.25 / 0.04
<i>Bouteloua gracilis</i> H.B.K. Lag	Blue Grama	G	5	0.79 / 0.38
<i>Carex filifolia</i> Nutt.	Threadleaf sedge	G	10	0.08 / 0.29
<i>Carex rossii</i> Boott	Ross sedge	G	11	0.00 / 0.17
<i>Festuca idahoensis</i> Elmer	Idaho fescue	G	10	1.00 / 1.00
<i>Festuca ovina</i> L.	Sheep fescue	G	10	0.00 / 0.08
<i>Helictotrichon hookeri</i> (Scribn.) Henr.	Spike oat	G	11	0.75 / 0.25
<i>Koeleria nitida</i> Nutt.	Junegrass	G	9	0.38 / 0.21
<i>Poa cusickii</i> Vasey	Cusick bluegrass	G	7	0.50 / 0.33
<i>Poa pratensis</i> L.	Kentucky bluegrass	G	7	0.21 / 0.00
<i>Poa secunda</i> Presl.	Sandbergs bluegrass	G	10	0.46 / 0.08
<i>Stipa comata</i> Trin. & Rupr.	Needle and thread	G	12	0.08 / 0.17
<i>Agropyron</i> spp.	Wheatgrass	G	8	0.04 / 0.04
<i>Selaginella densa</i> Rydb.	Compact spikemoss	M	n/a	0.84 / 1.00
<i>Xanthoparmelia wyomingica</i>	Rockfrog	M	n/a	0.36 / 0.02
<i>Peltigera rufescens</i>	Felt pelts	M	n/a	0.20 / 0.07
<i>Cladonia chlorophaea</i>	Peppered pixie-cup	M	n/a	0.75 / 0.61
<i>Cladonia pyxidata</i>	Pixie-cup	M	n/a	0.09 / 0.27
<i>Tortula ruralis</i>	Hairy screw moss	M	n/a	0.07 / 0.09
<i>Bryum caespiticum</i>	Moss	M	n/a	0.25 / 0.04

occurred on nearly every plot. Shallow-rooted forbs were dominated by both spring ephemeral forbs, including death camas (*Zigadenus venenosus* Wats.) and yellowbell (*Fritillaria pudica* Pursh), and midsummer bloomers, including penstemon (*Penstemon eriantherus* Pursh) and blanketflower (*Gaillardia aristata* Pursh). A single species of spikemoss, resurrection plant (*Selaginella densa*), accounted for 99% of the cover and biomass of the spikemoss group, while the mosses and lichens were rarer in occurrence and distribution.

Twenty-four species had a 75 percent or greater frequency of occurrence on both sites (Table 2.1). While most species were evenly distributed over both sites, there were some exceptions. *Iris missouriensis* had a frequency of occurrence of 90% at site 1 and was absent from site 2. Eight species had at least three times the frequency of occurrence on site 1 than site 2. Sixteen species were present on site 1 in low frequencies while absent from site 2. *Carex filifolia* and *Cladonia pyxidata* occurred on site 2 with at least three times the frequency as site 1. Five species were present on site 2 in low frequencies while absent from site 1.

Species density within a functional group and for the total plot was greater on site 2 than site 1 (Table 2.2). Grass tillers were about twice as dense on site 2 (434.6 tillers m^2) than site 1 (187.6 tillers m^2). This probably accounted for the greater overall density on site 2. While shallow-rooted forbs generally had a lower frequency of occurrence on site 2 than site 1, their density was about one third greater on site 2 (3.3 plants m^2) than site 1 (2.6 plant m^2).

Table 2.2. Means and P values generated from independent t-tests for species richness, density, Simpson diversity index and Shannon-Weaver Index at both sites.

Functional Group	Site	N	Density (m ²)	Biomass (gm ⁻²)	Richness (4 m ²)	Simpson Diversity Index	Shannon-Weaver Diversity Index
Grass	1	24	187.6	27.3	5.5	3.11	1.27
	2	24	434.6	29.7	4.0	1.66	0.65
	df		46	40	46	46	46
	P-value		<0.0001	0.303	<0.0001	<0.0001	<0.0001
Deep-rooted Forbs	1	32	1.9	47.5	10.8	4.95	1.85
	2	32	1.9	40.3	12.3	5.35	1.99
	df		62	32	62	62	62
	P-value		0.813	0.266	0.001	0.236	0.008
Shallow-rooted Forbs	1	32	2.6	23.5	26.9	12.56	2.81
	2	32	3.3	17.2	23.2	11.69	2.59
	df		62	32	62	62	62
	P-value		<0.0001	0.017	<0.0001	0.536	<0.0001
Total	1	16	22.9	89.1	43.6	4.28	1.86
	2	16	45.3	74.8	39.4	1.78	0.99
	df		30	30	30	30	30
	P-value		<0.0001	0.053	0.017	<0.0001	<0.0001

Site 1 had a greater total plot biomass (89.1 gm^{-2}) than site 2 (74.8 gm^{-2}); (Table 2.2). Shallow-rooted forbs accounted for 23.5 gm^{-2} (26%) and deep-rooted forbs 47.5 gm^{-2} (53%) of the plant community biomass at site 1. Site 2 had a greater biomass of grasses than site 1. Site 2 also had twice the biomass of the spikemoss functional group than site 1 (Table 2.3). *Selaginella densa* formed an almost continuous layer on the soil at site 2 (66 % cover), surrounding the base of bunchgrasses and had vascular vegetation growing through and within its foliage. In comparison, site 1 had more bare-ground.

Table 2.3. Mean richness, biomass and percent cover of mosses, lichens and spikemoss on both sites. The sample size per site was 56 for richness and percent cover, and 8 for biomass.

Functional Group	Site	Richness (4 m ²)	Biomass (gm ⁻²)	Percent Cover (m ²)
Moss / Lichen / Spikemoss	1	2.6	168	46
	2	2.1	366	66
	df	110	14	110
	P-value	0.009	0.002	<0.0001

Species diversity

Overall mean species richness within a 4 m^2 plot was 43.6 and 39.4 for sites 1 and 2, respectively (Table 2.2). Site 1 had greater species richness of the shallow-rooted forbs (26.9), grasses (5.5), and spikemoss (2.6) than what was recorded for site 2. Site 2 (12.3) had a greater richness of deep-rooted forbs than site 1 (10.8).

Two diversity indices were calculated for each site because the indices have different meaning of equatability (Table 2.2). For both indices, equatability increases with an increase in the index. According to the Simpson Index, the equatability of shallow- and

deep-rooted forbs did not differ statistically between sites. Site 1 ($D = 3.11$) had a greater Simpson Index for grass than site 2 ($D = 1.66$); therefore, grass species were more evenly distributed at site 1 than site 2. Total plot species diversity for site 1 ($D = 4.28$) was over two times greater than the diversity at site 2 ($D = 1.78$). The Shannon-Weaver Diversity Index indicated that the equatability of species within functional groups and the plot total differed between sites. At site 1, grasses, shallow-rooted forbs, and the total species per plot were more evenly distributed than at site 1. Evenness values ranged from $H = 1.27$ for grass, $H = 2.81$ for shallow-rooted forbs, and $H = 1.86$ for the plot total. As with the Simpson Index, site 2 ($H = 1.99$) had a greater evenness of deep-rooted forbs than site 1 ($H = 1.85$).

Soil characteristics

Soil classifications indicated site 1 soils are a loamy-skeletal, mixed, frigid, active Typic Haplocryolls (Haplo Cryic Mollisol), and site 2 soils are a coarse-loamy, mixed, frigid, active Typic Haplocryolls (Haplo Cryic Mollisol); (Table 2.4). Soil profile descriptions for each site showed small variations in the structure, material and pH of the A and Bw horizons. The main differences in the soil profiles were depth of the A horizon (22 verses 12 cm, site 1 and 2, respectively) and the presence of a Bw horizon at site 2. The Bw horizon structure, which contributed substantially to total profile depth, had larger, blockier soil aggregates (peds) than the A or Bk horizons of each site.

Table 2.4. Soil profile description for site 1 and site 2.

Site	Horizon	Depth	Structure	Material	pH	Reaction to acid
1	A Horizon	0- 22 cm	sub-angular-blocky, fine (5-10 mm) with 10% coarse fragments	sandy loam: 70% sand, 20% slit 10% clay	7.6	no reaction
	Bk Horizon	22-75 cm	sub-angular-blocky, fine to medium(5-20 mm) with 30% coarse fragments	sandy loam: 52% sand 42% silt 6% clay	8.4	violently effervescent
2	A Horizon	0-12 cm	sub-angular-blocky, fine (5-10 mm) with 10% coarse fragments	sandy loam: 70% sand 18% slit 12% clay	7.0	no reaction
	Bw Horizon	12- 37 cm	blocky, medium to coarse (20-50 mm) with 15-20% coarse fragments	sandy loam: 60% sand 32% silt 8% clay	7.2	no reaction
	Bk Horizon	37-75 cm	angular-blocky, fine to medium(5-20 mm) with 25% coarse fragments	sandy loam 60% sand 34% silt 6% clay	8.4	violently effervescent

Soil nutrients and water

At the 0-15 cm depths, mass water content, total N, $\text{NH}_4\text{-H}$, K, total soil C, and the C:N did not differ between sites 1 and 2 (Table 2.5). Site 1 had higher $\text{NO}_3\text{-H}$ and S levels and lower P levels in the shallow soils than site 2. The only difference between sites in nutrient concentration at 15-40 cm depths was $\text{NO}_3\text{-N}$ which was higher on site 1 than site 2 (3.38 verses 2.08 mg/kg, respectively).

All soil parameters were dependent on season, except K and percent total N which remained relatively constant for both depths and sites (Table 2.6). Seasonal depletion of the soil nutrients coincided with increased moisture (Figure 1). Mass water content and nitrate decreased from spring to fall for both sites at both soil depths. Other soil

Table 2.5. Mean mass water content and nutrient level differences between sites. All *t*-tests have 46 degrees of freedom.

Depth of soil (cm)		Mass Water Content (kg/kg)	Total Nitrogen (%)	Nitrate- N (mg/kg)	Ammonium- N (mg/kg)	Phosphorus (mg/kg)	Potassium (mg/kg)	Sulfur (mg/kg)	Total Carbon (%)	C:N (ratio)
Shallow (0-15)	Site 1	0.093	0.35	3.25	8.35	4.25	327	9.04	3.61	10.58
	Site 2	0.081	0.31	1.75	6.05	5.54	322	7.17	3.53	11.42
	P-value	0.145	0.062	0.013	0.171	0.011	0.635	0.047	0.588	0.058
Deep (15-40)	Site 1	0.106	0.26	3.38	8.61	3.58	305	7.00	2.70	10.50
	Site 2	0.105	0.23	2.08	5.54	3.46	289	7.46	2.51	11.21
	P-value	0.891	0.058	0.030	0.118	0.815	0.240	0.592	0.267	0.086

Table 2.6. Seasonal nutrient and mass water content for each soil depth at both sites. For each site and soil depth, means within columns with different letters are significantly different at $P \leq 0.05$ level. All cases have 23 total degrees of freedom.

Site	Soil Depth (cm)	Season	Soil Parameters								
			Mass Water Content (kg/kg)	Total Nitrogen (%)	Nitrate-N (mg/kg)	Ammonium-N (mg/kg)	Phosphorus (mg/kg)	Potassium (mg/kg)	Sulfur (mg/kg)	Total Carbon (%)	C:N (ratio)
1	Shallow (0-15)	Spring	0.105b	0.39a	4.63b	14.70b	5.88b	322a	12.25b	3.96a	10.5a
		Summer	0.112b	0.33a	3.63b	5.44a	3.13a	314a	7.50a	3.33a	10.0a
		Fall	0.061a	0.32a	1.50a	4.90a	3.75a	346a	7.37a	3.55a	11.3a
	Deep (15-40)	Spring	0.122b	0.27a	5.13b	14.78b	4.88a	293a	10.50b	2.79a	10.3a
		Summer	0.129b	0.26a	3.13b	5.72ab	2.75a	297a	5.50a	2.78a	10.6a
		Fall	0.068a	0.24a	1.88a	5.33a	3.13a	326a	5.00a	2.54a	10.6a
2	Shallow (0-15)	Spring	0.109c	0.31a	1.63ab	6.60a	5.50a	314a	7.13a	3.44a	11.0a
		Summer	0.084b	0.32a	2.25b	4.96a	6.38a	307a	6.25a	3.34a	10.9a
		Fall	0.049a	0.32a	1.37a	6.60a	4.75a	345a	8.13a	3.80a	12.4a
	Deep (15-40)	Spring	0.139c	0.21a	2.50b	6.34a	3.38b†	265a	8.13a	2.09a	10.3a
		Summer	0.118b	0.24a	2.50b	4.15a	4.50ab†	292a	7.63a	2.68b	11.3ab
		Fall	0.058a	0.24a	1.25a	6.11a	2.50a†	310a	6.63a	2.76b	12.1b

† Mann-Whitney nonparametric test was used because of unequal variance among groups.

Figure 2.1. Average monthly precipitation and temperature gathered from the Red Bluff Experimental Station, approximately 4 km from the research sites.

parameters tended to decrease from the spring to the fall but not consistently for both soil depths and sites. Ammonium levels decreased for site 1 shallow (14.70 to 4.90 mg/kg) and deep (14.78 to 5.33 mg/kg) depths from the spring to the fall. The magnitude of change in S content at site 1 soils decreased by approximately 5 mg/kg for each depth but did not vary significantly at site 2. Phosphorus decreased in site 1 shallow layers (5.88 to 3.75 mg/kg), and in site 2 deep layers (3.38 to 2.50 mg/kg). The C:N and percent C increased in site 2 deep layers from 10.3 to 12.1 and 2.09 % to 2.76%. The remaining parameters remained relatively constant across seasons.

Discussion

Site differences in plant community composition and soil nutrients support the tenant that soil substrate and nutrient levels regulate plant community composition (Clements 1920, Passey et al. 1982, MacCracken et al. 1983). Shallow-rooted forb richness and biomass on site 1 may account for greater resource acquisition in shallow depths (Lambers et al. 1998) and correlate with the seasonal decreases in soil nutrients seen on site 1 but not on site 2. The richness of shallow-rooted forbs on site 1 may also account for an increased rate of nutrient cycling and higher levels of $\text{NO}_3\text{-H}$ and S than site 2. Site 2 had a lower overall richness than site 1 but a greater density, richness, and diversity of deep-rooted forbs. The Bw soil zone at site 2 had a larger and more blocky structure than soils at site 1. The location of this zone in relation to the soil surface may make it more difficult for shallow-rooted forbs to acquire water and nutrients through mass flow allowing the deep-rooted forbs, whose roots can bypass this soil zone, to be

better site competitors (Tilman 1987, Gleeson and Tilman 1990). We attribute the greater biomass of deep-rooted forbs at site 1 to the higher occurrence of larger deep-rooted species, such as arrowleaf balsamroot. On site 2, lower $\text{NO}_3\text{-H}$ levels and large biomass tap-roots, compared to site 1, could be attributed to the seasonal increase in the C:N and total soil C (%) in deep layer. Seasonal depletion of the soil nutrients coincided with increased June moisture and the growth of shallow-rooted forbs.

Species diversity of both sites was high (Daubenmire 1970, Mueggler and Stewart 1980). Sampling over time allowed us to document greater species richness than previously suggested for this habitat type (Daubenmire 1970, Mueggler and Stewart 1980). In their classification description of the Idaho fescue/bluebunch wheatgrass habitat type in Montana, Mueggler and Stewart (1980) documented a total of 27 species of graminoids and 69 forb species from 45 sites. In comparison, we documented 14 graminoids and 69 forbs species from just two sites. It is hard to quantify the richness per site from Mueggler and Stewart; however, based the average constancy of each lifeform, 25% of the 27 grass species (7) and 24% of the 69 forb species (17) occurred on each of their 45 site. Similarly, Daubenmire (1970) documented an average of 3 grasses, 9 annual forbs and 8 perennial forbs per 4m^2 in the bluebunch wheatgrass/Idaho fescue habitat type of Washington. Our grassland description documented 39-44 species per plot 4m^2 which consisted of 4-6 grasses, 11-12 deep-rooted forbs, and 23-27 shallow-rooted forbs. We documented an average canopy cover of mosses/spikemoss/lichens of 46% and 66% which was comprised of 2-3 species. In comparison, Mueggler and Stewart (1970) estimated bryophytes to be 5-24% ground cover but did not identify species.

Our data also supported the hypothesis that forb functional groups represent the majority of the richness and biomass of the grassland community. Forbs accounted for 83% of the vascular species richness in our research. Similarly, Mueggler and Stewart (1980) and Daubenmire (1970) found 72% and 93% of the total species recorded for this habitat type to be forbs. Sims et al. (1978) found grasslands to be comprised of three to four times the number of forb species as grasses. In addition, forbs represented a greater proportion of plant biomass than the grasses on our sites. This was consistent with Mueggler and Stewart (1980) who found forbs account for approximately 1.5 times more biomass than grasses. The name 'grasslands' is misleading to the actual composition of this biome because grasses typically compose 20% or less of the total vegetative species richness (Sims and Risser 2000). Although three to four grass species may compose a large portion of the biomass in grasslands, the forbs contribute more to community diversity (Sims et al. 1978, Sims and Risser 1988). Because maintaining functional group diversity is critical to maintaining proper plant community functioning, more emphasis should be placed on managing grasslands for forb functional group diversity.

Our results indicate that greater species richness coincided with a greater overall biomass or productivity. This finding is congruent with other research suggesting increased diversity is positively correlated with increased community productivity and stabilization (Tilman et al. 1997, Tilman et al. 2001, Anderson and Inouye 2001, Naeem 1994) due to the more complete use of resources (Levine and D'Antonio 1999, Tilman 1997, Brown 1998, Carpinelli 2001). Lower availabilities of resources have been suggested to decrease invasibility of the community by undesired species (McNaughton

1993, Robinson et al. 1995). Recent research implies that functional diversity is as or more important to resisting invasion than species diversity alone (Symstad 2000, Dukes 2001, Tilman et al. 2001) because of resource preemption (Tilman 1997, Dukes 2001, Davis and Pelsor 2001, Levine and D'Antonio 1999, and Diaz and Cabido 2001).

Therefore, species number alone is not as important as species present with different ecosystem roles (Walker 1992, Diaz and Cabido 2001, Sala et al. 1996, Sheley et al. 1996) which suggests that ecosystem functioning may be sensitive to functional diversity.

Maintaining plant functional group diversity may be more important to ecological integrity than simply maintaining plant species diversity (Tilman et al. 1997, Hooper and Vitousek 1997, Power et al. 1996, Mack and D'Antonio 1998), because altering functional group diversity could materialize into large effects on ecosystem processes (Tilman et al. 1997, Diaz and Cabido 2001). Our dissection of the grassland plant community into functional groups was a means to investigate the diversity of forbs in the community. Dissection into functional groups was also a means to investigating the role of groups in plant community dynamics and management. We classified forbs into functional groups based on morphology because it reflects the life-history strategies of species (Lauenroth et al. 1978, Gitay and Noble 1997) and can be useful in predicting critical differences in ecosystem dynamics, such as, response to disturbance (Shaver et al. 1997, Gitay and Noble 1997), or changes in nutrient composition (Pickett et al. 1987, Connell and Slatyer 1977, Sheley et al. 1996). Besides being essential for ensuring the long-term persistence of all biota within a plant community (Walker 1992), managing for functional groups as management units may be more feasible than species-based

management. A land manager could classify functional groups according to the form and function of the vegetation within temporal and spatial scale of considerations (Woodward and Kelly 1997, Lauenroth et al. 1997) and their primary purpose (Westoby and Leishamn 1997). This allows the defining mechanism of the group to be monitored more directly and provides a link between the life history strategies at the plant level and the processes at the ecosystem level (Chapin 1993). Forbs are a diverse lifeform in grassland communities with various species persisting throughout the growing season. Separating forbs into functional groups is essential for understanding the direction of change within the plant community because groups are a stronger determinate of the ecosystem processes than the individual species diversity (Tilman et al. 1997).

Management Implications

We recommend land managers recognize forb species and forb functional group diversity in grassland classifications. Periodic field sampling during the growing season provides a better understanding of the plant community composition, and provides a target plant community for management. As a minimum, we recommend quantifying species diversity twice during the growing season. By sampling once in the spring, when arrowleaf balsamroot is beginning to bloom, and once in the summer, at peak standing crop, land managers should be able to capture approximately 83% of the diversity in the *Festuca idahoensis*/*Agropyron spicatum* habitat type. In comparison, 54% of community diversity was recorded with one field sampling.

We also recommend land managers establish and maintain forb species and forb functional group diversity in land management decisions. Intermediate levels of disturbance have been proposed to maintain the highest levels of diversity (Connell 1978). In land management, intermediate levels of disturbance can be obtained by regulating grazing timing and intensity, and through periodic prescribed burning. Diversity can also be maintained through careful planning of herbicide applications. We recommend calibrating herbicide rates to minimize effects on off-target plants, applying herbicides when the majority of indigenous vegetation are senescent, spot-spraying areas (versus area-wide spraying) to maintain diversity where individual plants exist, and reseeding competitive grasses and forbs after herbicide application.

Maintaining functional group diversity should be a primary objective of land managers because increased functional group diversity correlates with increased stability and productivity through niche differentiation and resource acquisition (Tilman 1997, Naeem 1994, Levine and D'Antonio 1999, Anderson and Inouye 2001). Increasing functional diversity also decreases the risk of invasion by undesired species (Symstad 2000, Dukes 2001). Indigenous forb functional groups use resources similarly to nonindigenous forb invaders and are a critical component in community invasion resistance (Kedzie-Webb et al. 2001, Chapters 3 and 4). Besides their contribution to ecosystem function, functional groups are a simpler management unit for managing diversity than a species-based approach because the goal is to establish and maintain multiple species which respond similarly to change and collectively resist invasion.

References

- Anderson, J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological Monographs* 71(2): 531-556.
- Begon, M., J. L. Harper, and C. R. Townsend. 1990. *Ecology: Individuals, Populations and Communities*, second edition. Blackwell Scientific Publications, Boston, MA.
- Brady, N.C., and R.R. Weil. 1999. *The Nature and Properties of Soil*. Prentice Hall, Upper Saddle River, New Jersey.
- Bremner, J. M. 1996. Nitrogen-Total. *In* *Soil Testing and Plant Analysis*. SSSA Book Series: 3. R. Westerman (ed.) Soil Science Society of America, Madison, Wisconsin.
- Brown, C. S. 1998. Restoration of California Central Valley grasslands: applied and theoretical approaches to understanding interactions among prairie species. Thesis (Ph.D.) University of California, Davis, California.
- Carpinelli, M. F. 2001. Designing weed-resistant plant communities by maximizing niche occupation and resource capture. Thesis (Ph.D.) Montana State University, Bozeman, Montana.
- Chapin, F. S. I. 1993. Functional role of growth forms in ecosystem and global processes. *In*: *Scaling Physiological Processes: Leaf to Globe*. J.R Ehleringer and C.B. Field (eds.) Academic Press. San Diego, California.
- Clements, F. E. 1920. *Plant Indicators, the relation of plant communities to process and practice*. Carnegie Inst. Wash. Publ., Washington.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111(982): 1119-1144.
- Cronquist, A., A. H. Holmgren, N. H. Holmgren, J. L. Reveal, and P. K. Holmgren. 1977. *Intermountain Flora; Vascular Plants of the Intermountain West, U.S.A.* Columbia University Press, New York., New York.

- Darwin, C. 1859. *The Origin of Species*. Reprinted by Penguin Books, London, UK.
- Daubenmire, R. 1970. *Steppe Vegetation of Washington*. Washington State University Cooperative Extension, Pullman, Washington.
- Davis, M.A., and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. *Ecology Letters* 4: 421-428.
- Diaz, S., and M. Cabido. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16(11): 646-655.
- Dorn, R. D. 1984. *Vascular Plants of Montana*. Mountain West Publishers, Cheyenne, Wyoming.
- Dukes, J. 2001. Biodiversity and invasibility in grassland microcosms. *Oecologia* 126: 563-568.
- Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. The University of Chicago Press, Chicago, Illinois.
- Flowers, S. 1973. *Mosses: Utah and the West*. Brigham Young University Press, Salt Lake City, Utah.
- Fuhlendorf, S.D., and D.M. Engle. 2001. Restoring heterogeneity of rangelands: ecosystem management based on evolutionary grazing patterns. *BioScience* 51(8): 625-632.
- Gitay, H., and I.R. Noble. 1997. What are functional types and how should we seek them? *In Plant Functional Types: their Relevance to Ecosystem Properties and Global Change*. T. M. Smith, H. H. Shugart, and F. I. Woodward (eds.). Cambridge University Press, Cambridge, UK.
- Gleeson, S. K., and D. Tilman. 1990. Allocation and the transient dynamics of succession on poor soils. *Ecology* 71(3): 1144-1155.
- Goodman, D. 1975. The theory of diversity-stability relationships in ecology. *The Quarterly Review of Biology* 50(3): 237-267.
- Hamm, J. W., J. R. Bettany, and E. H. Halstead. 1973. A soil test for sulphur and interpretative criteria for Saskatchewan. *Communications in Soil Science and Plant Analysis* 4:219-231.

- Helmke, P. A., and D. L. Sparks. 1996. Lithium, sodium, potassium, rubidium, and cesium. p. 551-574. *In* Soil Testing and Plant Analysis. SSSA Book Series: 3. R. Westerman (ed.) Soil Science Society of America, Madison, Wisconsin.
- Hogg, J. T., N. S. Weaver, J. J. Craighead, B. M. Steele, M. L. Pokorny, R. L. Redmond, and F. B. Fisher. 2001. Vegetative Patterns in the Salmon-Selwey Ecosystem: an Improved Land Cover Classification using Landsat TM Imagery and Wilderness Botanical Survey. Craighead Wildlife-Wildlands Institute, Missoula, MT.
- Hooper, D. U., and P. M. Vitousek 1997. The effects of plant composition and diversity on ecosystem processes. *Nature* 277: 1302-1305.
- Jensen, M. E., L. S. Peck and M. V. Wilson. 1988a. A sagebrush community type classification for mountainous northeastern Nevada rangelands. *Great Basin Naturalist* 48(4): 422-433.
- Jensen, M. E., L.S. Peck and M. V. Wilson. 1988b. Vegetation characteristics of mountainous northeastern Nevada sagebrush community types. *The Great Basin Naturalist* 48(4): 403-412.
- Jones, J. B., Jr. 1977. Elemental analysis of soil extracts and plant tissue ash by plasma emission spectroscopy. *Communications in Soil Science and Plant Analysis*. 8:349-365.
- Kearney, T. H., L. J Briggs, H. L. Shantz. 1914. Indicator significance of vegetation in the Toole Valley, Utah. *J. Agric. Res.* 1: 365-417.
- Kedzie-Webb, S. A., R. L. Sheley, J. J. Borkowski, and J. S. Jacobs. 2001. Relationships between *Centaurea maculosa* and indigenous plant assemblages. *Western North American Naturalist* 61(1): 43-49.
- Lambers, H., F. S. Chapin III, T. L. Pons. 1998. *Plant Physiological Ecology*. Springer-Verlag, New York, New York.
- Lauenroth, W. K., J. L. Dodd, and P. L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia* 36: 211-222.

- Lauenroth, W. K., D. P. Coffin, I. C. Burke, and R. A. Virginia. 1997. Interactions between demographic and ecosystem processes in a semi-arid and an arid grassland: a challenge for plant functional types. *In* Plant Functional Types: their Relevance to Ecosystem Properties and Global Change. T. M. Smith, H.H. Shugart, and F.I. Woodward (eds.), pp. 234-254. Cambridge University Press, Cambridge, UK.
- Leyne, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of the evidence linking diversity and invasibility. *Oikos* 87: 15-26.
- MacArthur, R. H. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- MacCracken, J. G., D.W. Uresk, and R. M. Hansen. 1983. Plant community variability on a small area in southeastern Montana. *Great Basin Naturalist* 43(4): 660-668.
- Mack, M.C., and C.M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13(5): 195-198.
- McCune, B. 1995. *Macrolichens of the Northern Rocky Mountains*. Mad River Press, Eureka, California.
- McNaughton, S. J. 1993. Biodiversity and function of grazing ecosystem. *In* Biodiversity and Ecosystem Function. E. D. Schulze, and H. A. Mooney (eds.), pp. 363-383. Springer-Verlag, New York, New York.
- Mueggler, W. F., and W. L. Stewart. 1980. *Grassland and Shrubland Habitat Types of Western Montana*. Intermountain Forest and Range Experimental Station, Ogden, Utah.
- Mulvaney, R. L. 1996. Nitrogen- Inorganic Forms. *In* Soil Testing and Plant Analysis. SSSA Book Series: 3. R. Westerman (ed.) Soil Science Society of America, Madison, Wisconsin.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. W. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734-737.
- Nelson, D. W., and L. E. Sommers. 1996. Total Carbon, Organic Carbon, and Organic Matter. *In* Soil Testing and Plant Analysis. SSSA Book Series: 3. R. Westerman (ed.) Soil Science Society of America, Madison, Wisconsin.

- Olsen, S. R., C. V. Cole, F. S. Watanabe, and L. A. Dean. 1954. Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate. USDA Circ. 939. USDA, Washington, DC. USA.
- Passey, H. B., V. K. Hugie, E. W. Williams, and D. E. Ball. 1982. Relationships between soil, plant community, and climate on rangelands of the Intermountain West. US Department of Agriculture, Technical Bulletin 1669. Fort Collins, Colorado.
- Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms and pathways of succession. *The Botanical Review*. 53(3): 335-371.
- Pimm, S. L. 1991. *The balance of nature?* University of Chicago Press, Chicago, Illinois.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience*. 46(8):609-620.
- Robinson, G. R., J. F. Quinn, and M. L. Stanton. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* 76(3): 786-794.
- Sala, O. E., W. K. Lauenroth, S. J. McNaughton, G. Rusch, and X. Zhang. 1996. Biodiversity and ecosystem function in grasslands. John Wiley & Sons, Chichester, Massachusetts.
- Shantz, H. L., and R. L. Piemeisel. 1924. Indicator significance of the natural vegetation of the southwestern desert. *J. Agric. Res.* 28: 721-802.
- Shaver, G. R., A. E. Giblin, K. T. Nadelhoffer, and E. B. Rastetter. 1997. Plant functional types and ecosystem change in arctic tundras. *In* Plant Functional Types: their Relevance to Ecosystem Properties and Global Change. T. M. Smith, H.H. Shugart, and F.I. Woodward (eds.), pp. 153-173. Cambridge University Press, Cambridge, UK.
- Sheley, R. L., T. J. Svejcar, and B.D. Maxwell. 1996. A theoretical framework for developing successional weed management strategies on rangeland. *Weed Technology* 10: 766-773.
- Sims, P. L., J. S. Singh, and W. K. Lauenroth. 1978. The structure and function of ten Western North American grasslands: I. Abiotic and Vegetative Characteristics. *Journal of Ecology* 66: 251-285.

- Sims, P. L., and P. G. Risser. 2000. Grasslands. *In* North American Terrestrial Vegetation, vol. 2. Barbour, M.G. and W.D. Billings (eds.), pp. 323-395. Cambridge University Press, Cambridge, UK.
- SPSS Inc. 1999. Base 10.0 Users Guide. Chicago, Illinois.
- Stoddart, L. A., and A. D. Smith. 1943. Range Management. McGraw-Hill Book Co. Inc., New York, New York.
- Symstad, A. J. 2000. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* 81(1): 99-109.
- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* 57(3): 189-214.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78(1): 81-92.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem process. *Science* 277: 1300-1305.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294(26): 843-845.
- Walker, B. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6(1): 18-23.
- Westoby, M., and M. Leishman. 1997. Categorizing plant species into functional types. *In* Plant Functional Types: their Relevance to Ecosystem Properties and Global Change. T. M. Smith, H. H. Shugart, and F. I. Woodward (eds.), pp. 104-121. Cambridge University Press, Cambridge, UK
- Willoughby, M. G., M. J. Alexander, and K. M. Sundquist. 1998. Range Plant Community Types and Carrying Capacity for the Montane Subregion, 3 edition. Environmental Protection Lands and Forest Services, Edmonton, Alberta.
- Woodward, F. I., and C. K. Kelly. 1997. Plant functional types: towards a definition by environmental constraints. *In* Plant Functional Types: their Relevance to Ecosystem Properties and Global Change. T. M. Smith, H.H. Shugart, and F.I. Woodward (eds.), pp. 47-65. Cambridge University Press, Cambridge

CHAPTER 3

ROLE OF FUNCTIONAL GROUP DIVERSITY IN RESISTING INVASION
IN A GRASSLAND PLANT COMMUNITYIntroduction

Invasive nonindigenous plants dominate millions of hectares throughout the western United States (Sheley and Petroff 1999). These weeds may be permanently altering the structure and function of indigenous ecosystems (Sheley et al. 1998, Mack and D'Antonio 1998, Olson 1999). Research suggests invasive species can degrade soil and water resources (Lacey et al. 1989, Sheley et al. 1997), reduces wildlife and livestock habitat and forage (Hakim 1979, Kurtz et al. 1995), and alter community structure by decreasing the density, biomass, and basal area associated with indigenous plant communities (Olson 1999, Christain and Wilson 1999, Kedzie-Webb et al. 2001).

Susceptibility of grasslands in the western United States to invasion may be influenced by many factors, including community structure (Orains 1984), resource availability (Elton 1958, Burke and Grime 1996, Tilman 1997, and Stohlgren et al. 1999) and invader traits (Davis and Pelsor 2001). Alien species belonging to nonindigenous genera may be more likely to successfully invade native plant communities than nonindigenous genera (Darwin 1859, Rejmanek 1996). Most nonindigenous plants invade areas of similar latitude as their native occurrences; however, invaders may be fundamentally different in species function from the local vegetation (Rejmanek 1996, Rejmanek and Richardson 1996, Callaway and Aschehoug 2000). Nonindigenous species

may have genetic and life-history traits that allow them to preempt resources more rapidly or to a lower level than indigenous vegetation, allowing them to become successful invaders (Roy 1990, Rejmanek 1996, LeJeune and Seastedt 2001, Sakai et al. 2001).

Ecologists have recognized the importance of diverse plant communities in maintaining vigorous ecosystems (MacArthur and Wilson 1967, Goodman 1975, Pimm 1991). A number of researchers have suggested that chances of alien plant invasion decreases with increased indigenous species diversity (Elton 1958, Burke and Grime 1996, McGrady-Steele et al. 1997, Tilman 1997), while others maintain that species-poor communities resist invasion better than species diverse communities (Robinson et al. 1995, Stohlgren et al. 1999, Levine and D'Antonio 1999). The discrepancy of positive versus negative effects of species diversity may be scale dependent (Prieur-Richard and Lavorel 2000). For example, Stohlgren (1999) found opposite correlation between diversity and invasibility when going from a local to regional scale. It is also possible that species are redundant in function so that species richness alone may be irrelevant to invasion resistance (Lawton and Brown 1993, Diaz and Cabido 2001).

Increasing evidence suggests that plant functional group diversity is more important to ecological integrity than plant species diversity (Walker 1992, Power et al. 1996, Sala et al. 1996, Tilman et al. 1997, Hooper and Vitousek 1997, Mack and D'Antonio 1988, Diaz and Cabido 2001). A functional group of species share physiological and morphological traits, and provide a link between the physiological and life history strategies at the plant level and the processes at the ecosystem level (Lauenroth et al. 1978, Chapin 1993). The greater the functional diversity, the less chance for

redundancy in ecosystem function in the plant community. This has important implications in managing for weed-resistant grasslands. For example, increasing functional diversity has been shown to decrease invasion by nonindigenous invaders through maximizing niche occupation and preempting available resources (Brown 1998, Dukes 2001, Carpinelli 2001).

Because a generalized objective for invasive plant management is to establish and maintain weed resistant plant communities that meet other land-use objectives (Sheley et al. 1996), understanding and identifying which functional groups, or combinations of functional groups, resist invasion from nonindigenous species is critical. Some experimental evidence suggests functionally similar species compete and resist each other more than non-similar species (Dukes 2001), but in some cases, this evidence is weak (Symstad 2000). Furthermore, some experiments suggest that species diversity within functional groups is needed for community stability (Tilman et al. 2001) while other research contradicts this notion (Dukes 2001). To decrease and manage invasions, mechanisms contributing to invasion resistance must be identified and incorporated into management programs.

The overall objective of this research was to investigate the role of functional groups and functional group diversity in resisting invasion by a nonindigenous species. Our specific objectives were 1) to test the invasibility of communities with varying functional group diversities by the nonindigenous invader *Centaurea maculosa* Lam. (spotted knapweed), 2) compare the ability of various indigenous functional groups in resisting invasion, 3) to determine the influence of *C. maculosa* on the biomass of

indigenous functional groups, and 4) to investigate the degree of variability of a functional groups biomass in the community. We chose to work with *C. maculosa* because it is an abundant and widely distributed nonindigenous forb in the western United States. Although we focus on one nonindigenous species in this research, other deep-rooted nonindigenous forbs may act similarly.

We hypothesized that removing a functional group would yield higher *C. maculosa* densities and biomass than the control, and that *C. maculosa* density and biomass would increase as functional groups were progressively removed. Our rationale for this hypothesis is that more resources would be available in unfilled niches in the plant community for the invader to use. We also hypothesized that removing forb functional groups would increase *C. maculosa* biomass and density more than removing grasses, because indigenous and nonindigenous forbs may share physiological and morphological traits and, perhaps, ecosystem function. *Centaurea maculosa* has completely dominated plant communities in the western United States. Therefore, we predicted that its presence would lower the biomass of individual indigenous functional groups and total plot biomass. Individual functional groups biomass was investigated to quantify a groups contribution to total community biomass, determine the variability of functional group composition in the community throughout the growing season, and determine if removal treatments effected a plots total biomass.

Methods

Study sites

This study was conducted on two sites within the *Festuca idahoensis*/*Agropyron spicatum* (Idaho fescue/bluebunch wheatgrass) habitat type (Mueggler and Stewart 1980). This habitat type lies at the cool-wet end of grassland habitat types and is widely distributed throughout the mountain grasslands in southwestern Montana and the western United States, providing an excellent model for applied ecological research. Besides the perennial grasses *Festuca idahoensis* Elmer and *Agropyron spicatum* Pursh., predominant indigenous forbs include *Artemisia ludoviciana* Nutt. (prairie sage), *Balsamorhiza sagittata* Nutt. (arrowleaf balsamroot), and *Lupinus* spp. (Lupine), although the proportion of forbs varies with location for this habitat type (Mueggler and Stewart 1980). Medium shrubs are absent from this habitat type unless it has been severely disturbed. Our specific sites were chosen because they were near enough to one another to be considered similar.

Sites were located on the Flying D Ranch approximately 70 km east (45°34' N, 111° 34' W) of Bozeman, Montana. Sites lie on an east-northeast aspect of a 20 degree slope at 1,624 m elevation. Prior to plot establishment, soils were tested for the presence of picloram (4-amino-3,5,6-trichloropicolinic acid, potassium salt) to minimize the risk that site characteristics and plant community composition were influenced by recent herbicide applications. Picloram was not detected at a level of 0.01 mg/kg. Site 1 soils were a loamy-skeletal, mixed, frigid, active Typic Haplocryolls (Haplo Cryic Mollisol) and

site 2 soils were a coarse-loamy, mixed, frigid, active Typic Haplocryolls (Haplo Cryic Mollisol). Annual average precipitation is 41 cm with peaks in the spring and fall. Annual average temperature ranges from 5.5 to 7°C.

The area has been grazed for decades, and in some years it has been heavily grazed, by either cattle or bison (*Bison bison*) in its recent history (50-60 years). Bison grazing during the past ten years has been sporadic. Windblown slopes are prime winter habitat for wildlife. In the study area, winter use by elk (*Cervus elaphus*) has steadily increased as herd size increased during the past 20 years. In 2000, each site was fenced with a 2 meter, eight strand fence to prevent grazing by livestock and wildlife.

Experimental design

Species of grass, forbs, and spikemoss were combined into functional groups based on morphological and physiological similarities. Forbs were further divided into two functional groups based on average rooting depth. Prior to removing any species, all forbs were carefully excavated and their root structure and rooting depth determined. The distinction between a shallow and a deep depth was based on a natural break within the roots sampled which occurred at 15 cm. In cases where the average root depth was close to 15 cm, species with primarily fibrous roots were considered shallow-rooted, while tap-roots were grouped with deep-rooted forbs. The nonindigenous species, *C. maculosa*, is a late-season, deep-rooted forb from Eurasia (Jacobs and Sheley 1998) and was considered its own functional group.

Treatments, arranged in a randomized-complete-block design, were applied by removing one or more functional groups from 2 x 2 m plots. The experiment was a complete factorial design, with 7 removal treatments, 2 nonindigenous invader treatments, 2 sites, and 4 blocks, for a total of 112 plots. The seven removal treatments included removal of: 1) nothing (control), 2) moss, lichens and fern allies (collectively referred to as spikemoss throughout the paper), 3) shallow-rooted forbs, 4) deep-rooted forbs, 5) all grasses, 6) all forbs, and 7) all plant material. The two nonindigenous invader treatments were 1) *C. maculosa* absent and 2) *C. maculosa* present. Removal treatments were applied in the spring of 2000 and plot diversity was maintained biweekly throughout the 2000 and 2001 growing seasons.

Functional groups were removed by carefully brushing a 6% glyphosate, [N-(phosphonomethyl) glycine] solution on foliage of target species, minimizing disturbance to surrounding soil and plant community. After plants died, the remaining aboveground plant material was clipped at ground level and removed from the plot to minimize nutrient leaching from plants to soil. We chose plant removals over additions because experimental removals is the most convincing way of determining interaction strengths (Wootton 1994) and inter-taxa competition (Goelz 2001), and because of the time required to establish mature plant communities. Through plant removals and addition of *C. maculosa* seeds, we eliminate the possibility that the invader has altered the plant and soil community, and the invasion reflects the features of the community, not the propagule supply (Levine and D'Antonio 1999).

During September and October 2000, the nonindigenous invader treatments were applied by seeding *C. maculosa* on one-half the plots. *Centaurea maculosa* seeds were collected in August 2000 from Plains, Montana (47°28' N, 114° 53' W). Prior to seeding, seeds were cleaned of insects, vegetative material, and other seeds using a South Dakota Seed Blower (Hoffman Manufacturing Company). Seed germination and viability rate (AOSA 2000) were 55% and 94%, respectively. *Centaurea maculosa* seeds were broadcast biweekly from September 19 to October 31 to mimic natural seedrain (Sheley et al. 1997). Seeding rate, based on the life-history study of Jacobs and Sheley (1998) and Sheley et al. (1997), totaled 2,000 seeds m⁻², or 8,000 seeds per plot.

Sampling and data collection

Species richness was recorded biweekly through the 2000 growing season on all plots where no plants were removed (control) and where all plant material was removed. For all other treatments, presence was determined for the plant material removed. All forb species were identified using Dorn (1984), while grasses follow the nomenclature of Cronquist et al. (1977).

Centaurea maculosa density was counted in the spring, summer, and fall of 2001 over the entire 2 x 2 m plot. Spring sampling occurred when the majority of the spring ephemeral forbs were blooming, summer sampling coincided with peak standing crop, and fall sampling occurred after 95% of the vegetation was senescent. Functional group biomass was collected at each of the three sampling periods. Plots were divided into three subplots which were randomly assigned to either of the spring, summer, or fall sample

periods during 2001. Functional group biomass was collected within three 0.2 x 0.5 m frames randomly located within the subplots. *Centaurea maculosa* biomass was collected only in the fall of 2001 because harvesting during the spring and summer would have affected seedling establishment. All above-ground current-year growth was harvested at ground level by functional group. Spikemoss biomass was removed as part of the treatments and was not removed in subplots. Plant material was dried (40 °C, 160 hours) to a constant weight and biomass was recorded.

Data Analysis

For all analyses, sites were analyzed separately because of initial differences in plant community composition and soil nutrient levels. Test results were considered significant at the $\alpha \leq 0.05$ level.

Analysis of variance (ANOVA) was used to test the hypotheses that increased functional group removals would increase *C. maculosa* density and biomass. First, ANOVA was used to determine effects of removal treatment, season, and block and a removal treatment*season effect on *C. maculosa* density. Square root transformations were used to meet the assumption of equal variances. Block*removal treatment was added to the error term when no significant differences were found. The error term included removal treatment*season*block plus block*removal treatment and had 60 degrees of freedom. Multiple comparisons were achieved using Tukey post-hoc tests (Zar 1999) in SAS (SAS 1990). *Centaurea maculosa* biomass was analyzed using ANOVA. Site 1 data was transformed to the square root biomass and site 2 was transformed to the

reciprocal to meet the assumptions of equal variance. Removal treatment and block were main effects. The error term had 18 degrees of freedom.

ANOVAs with repeated contrasts (Zar 1999) were used to analyze differences in a functional group's biomass between plots where *C. maculosa* was present versus plots where this invader was absent. One model compared the total plot biomass (minus *C. maculosa*) of a specific treatment with and without *C. maculosa*. For example, the biomass of all forbs in plots where grasses were removed was contrasted with the biomass of all forbs in plots where grasses were removed and *C. maculosa* was added. Another model compared the biomass of each functional group grown in the presence and absence of *C. maculosa*.

ANOVA was also used to test the effects of removals on total plot biomass. Removal treatment was the main effect and the error term had 36 degrees of freedom. Biomass of each functional group was analyzed using ANOVA. In this case, functional groups, season, and block were all main effects and functional group*season was the interaction term. Tukey's multiple comparisons were calculated in SAS.

Results

Functional group and total plot biomass

Ninety plant species were identified in this grassland system. Of those species, forty-seven were shallow-rooted forbs, 22 were deep-rooted forbs, 14 were grasses, 4 were lichens, 1 was a spikemoss, and 2 were mosses. Shallow-rooted forbs (0-15 cm roots) consisted of annual and perennial species with bulbs, rhizomes, fibrous roots and/or

shallow tap-roots. Deep-rooted forbs (15-40+ cm roots) were primarily perennial tap-rooted plants with varying lateral root lengths and depths.

We were interested in the natural variability and distribution of the functional groups biomass over the three seasons in diverse grassland communities and found that biomass at site 1 varied among functional groups and with season (Table 3.1). Deep-rooted forbs had a greater biomass (48 gm^{-2}) than shallow-rooted forbs (24 gm^{-2}) and grass (27 gm^{-2}) at site 1 (Table 3.2). The highest functional group biomass occurred in the fall while biomass of functional groups was lowest during the spring (Table 3.2). On site 2, the amount of biomass depended on functional group, season, and a functional group*season interaction (Table 3.1). All three functional groups yielded similar biomass in the spring (Figure 3.1). In the summer, grasses (30 gm^{-2}) and deep-rooted forbs (36 gm^{-2}) had a greater biomass than shallow-rooted forbs (16 gm^{-2}). Deep-rooted forbs produced higher biomass (65 gm^{-2}) than either of the other two functional groups in the fall. Fall biomass for grass and shallow-rooted forbs was 36 gm^{-2} and 23 gm^{-2} , respectively. Deep-rooted forbs was the only group whose biomass varied seasonally with an increase in biomass from the spring (20 gm^{-2}) to the summer (60 gm^{-2}). Biomass of spikemoss on plots was not used for the analysis of variance because it does not represent the groups seasonal biomass (Mueggler and Stewart 1980, van Tooren et al. 1990). Instead the biomass of spikemoss removed from plots when treatments were applied was dried and weighed. Mean spikemoss biomass was 168 gm^{-2} for site 1 and 366 gm^{-2} for site 2. ANOVA contrasts found no differences between a functional groups biomass in the presence or absence of *C. maculosa* on either site. Data not shown.

Table 3.1. ANOVA results for functional group, season, and block effects on functional group biomass at sites 1 and 2.

Source	df	Site 1		Site 2	
		Mean Square	P-value	Mean Square	P-value
Functional Group	2	1467.1	<0.0001	1156.5	<0.0001
Season	2	1312.2	<0.0001	1226.2	<0.0001
Block	3	20.7	0.834	30.4	0.408
FGroup*Season	4	54.9	0.548	284.2	<0.0001
Error	300	71.8	n/a	31.4	n/a

Table 3.2. Mean separations for biomass main effects at site 1. Letters represent significant differences at the $\alpha \leq 0.05$ level. Functional group biomass is average over seasons. Seasonal biomass is the average of the grass, shallow-, and deep-rooted forbs functional groups.

Dependent Variable		Biomass (gm ²)	Std. Error	95% Confidence Interval	
				Lower Bound	Upper Bound
Functional Group	Grass	27.34a	1.80	23.78	30.89
	Shallow-rooted Forbs	23.55a	1.89	19.80	27.30
	Deep-rooted Forbs	47.52b	4.60	38.39	56.64
Season	Spring	19.18a	1.55	16.10	22.26
	Summer	36.67b	3.36	29.00	42.34
	Fall	42.29b	3.45	35.45	49.14

At both sites, each removal treatment had a similar total plot biomass regardless of *C. maculosa* presence or absence (data not shown). Therefore, we focus on the total biomass of plots where functional groups were removed and *C. maculosa* was added for these results and the discussion (Figure 3.2). Total plot biomass after functional groups were removed depended on removal treatment at both sites (site 1: $F_{5,18} = 4.35$, $p = 0.009$,

Figure 3.1. Seasonal functional group biomass collected during the 2001 growing season at site 2. Letters represent differences ($P < 0.05$) among functional groups biomass, comparable within a given season. Error bars (Std error) represent seasonal differences in a functional groups biomass.

Figure 3.2. Total plot biomass per removal treatment at sites 1 and 2. Removal treatments were initiated in spring 2000 and means represent the seasonal average for 2001. Letters represent significant differences within a site at the 0.05 level. *C. maculosa* (denoted KW) was seeded in removal treatments during fall 2001.

site 2: $F_{5, 18} = 5.28$, $p = 0.004$). Plots where all forbs were removed had a lower total plot biomass (30 gm^{-2}) than plots where spikemoss (97 gm^{-2}) or grasses (89 gm^{-2}) were removed. All other treatments on site 1 had a similar total plot biomass, averaging 57 gm^{-2} . At site 2, plots where all forbs were removed had a lower total plot biomass (33 gm^{-2}) than plots where nothing was removed (mean of 82 gm^{-2}), plots where spikemoss was removed (69 gm^{-2}), and plots where grasses were removed (68 gm^{-2}). All other treatments on site 2 had a similar total plot biomass.

Centaurea maculosa density and biomass

The influence of removal treatments on *C. maculosa* density depended upon the season at both sites (Table 3.3). At site 1, removal treatments did not influence *C. maculosa* density in the spring (Figure 3.3). Spring *C. maculosa* density averaged 4 plants m^{-2} . *Centaurea maculosa* density increased from spring to summer for all treatments. In the summer, the highest *C. maculosa* density occurred where all plant material was removed (56 plants m^{-2}). Removing spikemoss, shallow-rooted forbs, and all forbs produced similar summer *C. maculosa* densities, averaging around 26 *C. maculosa* plants m^{-2} . Treatments where nothing (3 plants m^{-2}), deep-rooted forbs (4 plants m^{-2}), or grasses (10 plants m^{-2}) were removed had the lowest summer *C. maculosa* densities. *Centaurea maculosa* density on plots where nothing, spikemoss, shallow-rooted forbs, deep-rooted forbs or grasses were removed decreased from the summer to the fall to levels similar to spring densities (average 1 plant m^{-2}). In the fall, removal treatments where all plant material or all forbs were removed had the highest *C. maculosa* densities

(41 and 16 plants m^{-2} , respectively). The lowest *C. maculosa* densities in all three seasons occurred on plots where nothing, the deep-rooted forbs, or grasses were removed.

On site 2, response of *C. maculosa* density to removal treatments was similar as site 1 (Figure 3.4). In the spring, all treatments had a similar *C. maculosa* density (2 to 6 plants m^{-2}) except where all plant material was removed at site 2. Removing all plants produced an average of 67 *C. maculosa* seedlings m^{-2} . *Centaurea maculosa* density increased from spring to summer on all treatments except where no plant material or all plant material was removed. The control, where all functional groups existed, had the lowest summer density of *C. maculosa* density (3 plants m^{-2}), while plots where all plant material was removed had the highest summer *C. maculosa* density (80 plants m^{-2}). In addition, plots where all forbs were removed had 30 *C. maculosa* plants m^{-2} which was similar to the *C. maculosa* density of plots where spikemoss was removed (16 plants m^{-2}) that season. Removal of deep-rooted forbs and grasses had a similar effect on the summer *C. maculosa* density (average 12 plants m^{-2}). When shallow-rooted forbs were removed, the summer *C. maculosa* density (8 plants m^{-2}) was similar to all treatments except where all forbs or all plant material was removed. *Centaurea maculosa* density declined from the summer to the fall for all treatments except where all forbs or grasses were removed on site 2. Treatments producing highest fall densities of *C. maculosa* were where all plant material was removed (56 plants m^{-2}) and where all forbs were removed (22 plants m^{-2}). Treatments where nothing, spikemoss, shallow-rooted forbs, deep-rooted forbs, or grasses were removed had similar *C. maculosa* densities as in the spring (average 2.6 plants m^{-2}) at site 2.

Figure 3.3. *Centaurea maculosa* densities for site 1 where functional groups had been removed. Removal treatments were initiated in spring 2000 and means are from 2001. Letters represent density differences among treatments at the $P < 0.05$ level. Superscript letters represent seasonal density differences within a treatment.

Figure 3.4. *Centaurea maculosa* densities for site 2 where functional groups had been removed. Removal treatments were initiated in spring 2000 and means are from 2001. Letters represent density differences among treatments at the $P < 0.05$ level. Superscript letters represent seasonal density differences within a treatment.

Centaurea maculosa biomass depended on removal treatment at both sites (Table 3.4). Removing all plant material produced the highest *C. maculosa* biomass on site 1 (12.5 gm^{-2}) and on site 2 (99 gm^{-2}); (Figure 3.5). On plots where all forbs were removed, *C. maculosa* biomass was 2 gm^{-2} and 4 gm^{-2} for site 1 and 2, respectively. At site 1, *C. maculosa* biomass was similar on plots where shallow-rooted forbs, grasses, or all forbs were removed, averaging 1 gm^{-2} . On site 2, removing deep-rooted forbs produced a similar *C. maculosa* biomass as removing all forbs, 0.4 gm^{-2} and 4 gm^{-2} , respectively. All other treatments per site had a similar *C. maculosa* biomass ranging from $0\text{-}0.5 \text{ gm}^{-2}$.

Table 3.3. P-values and mean squares for the square root *Centaurea maculosa* density.

Source	df	Site 1		Site 2	
		Mean Square	P-value	Mean Square	P-value
Treatment	6	109.44	<0.0001	280.79	<0.0001
Season	2	182.89	<0.0001	91.87	<0.0001
Block	3	3.54	0.285	2.35	0.368
Treatment*Season	12	20.46	<0.0001	9.89	0.020
Error	60	2.74	n/a	2.19	n/a

Table 3.4. ANOVA results for the square root *Centaurea maculosa* biomass on site 1 and the reciprocal *C. maculosa* biomass on site 2.

Source	df	Site 1		Site 2	
		Mean Square	P-value	Mean Square	P-value
Treatment	6	1.87	<0.0001	0.50	<0.0001
Block	3	0.31	0.007	0.01	0.625
Error	18	0.06	n/a	0.01	n/a

Figure 3.5. *Centaurea maculosa* biomass in plots where functional groups had been removed at sites 1 and 2. Removal treatments were initiated in spring 2000 and means are from fall 2001. Letters represent biomass differences among removal treatments at the $P < 0.05$ level.

Discussion

Functional group and total plot biomass

Forbs represented a greater proportion of plant biomass than grasses on our sites which was consistent with Mueggler and Stewart (1980) Idaho fescue/ bluebunch wheatgrass habitat description where forbs accounted for approximately 1.5 times more biomass than grasses. The robust, deep-rooted forbs dominated the biomass on site 1 and were a large contributor to the overall community biomass in all three seasons on site 2. Biomass of the shallow-rooted forbs in this grassland community has been underestimated in land management practices. This group is typically characterized as small, spring ephemeral plants. Our data suggests that even though small, these species are ubiquitous enough to comprise roughly one-fourth of the total biomass on both sites. Furthermore, shallow-rooted forb biomass was well represented throughout the entire growing season and were not merely spring ephemeral forbs.

Some variation in total plot biomass was expected due to the variability in functional groups present per treatment (Mueggler and Stewart 1980). It was reasonable to believe that removing one or two functional groups contributing a large portion of the communities' biomass would decrease total plot biomass and affect community stability (Tilman et al. 1996, Tilman et al. 1997, Hooper and Vitousek 1997). For example, natural disturbances can cause decreases in indigenous vegetation biomass and increases in a nonindigenous invader biomass (Pokorny et al. 2001). In this study, a treatments total plot biomass and *C. maculosa* density and biomass seemed to be unrelated. Therefore, *C.*

maculosa establishment was not biased by overall plot productivity but may instead be associated with restructuring functional group diversity and composition (Symstad 2000).

Our results suggest that functional group biomass and total plot biomass was resilient to change by *C. maculosa*, therefore we rejected our hypothesis that a nonindigenous invader decreases the biomass of indigenous functional groups. This was a surprising result because grasslands heavily invaded by *C. maculosa* have had a change in the organization and structure of the indigenous plant community (Olsen 1999). We believe *C. maculosa* may not have negatively effected the indigenous biomass because it is in an initial establishment stage and may not have extended its complete influence.

Continued monitoring of indigenous plant biomass will investigate long-term changes between the biomass of functional groups in the presence and absence of *C. maculosa*. Thus, lack of negative impact of *C. maculosa* on the indigenous plant biomass may be due to the competitive ability of indigenous functional groups and/or the lack of interspecific competition occurring in *C. maculosa*'s early stage of development.

Centaurea maculosa density and biomass

Our results are consistent with a growing body of evidence suggesting increased functional diversity decreases invasion through the preemption of available resources (Sheley et al. 1998, Levine and D'Antonio 1999, Tilman et al. 1996, Davis and Pelsor 2001, Diaz and Cabido 2001, Dukes 2001). Work by Stohlgren et al. (1999) and Robinson et al. (1995) found that species-poor communities resist invasion better than species rich communities. Both studies focused on species diversity rather than functional

diversity. It is possible that each species in species-poor communities differed in function and/or had a particular species present increased resistance to invasion. We focused on functional group diversity because it accounts for redundancy in ecosystem function among species, and may be a better test for measuring invasion resistance. In our study, *C. maculosa* density and biomass was higher at lower levels of functional group diversity on both sites. Similarly, in grassland community microcosms, Dukes (2001) found high functional diversity reduced the success of an invader by decreasing resource availability, and in a tallgrass prairie ecosystem, Symstad (2000) found a negative relationship between functional group richness and invasion success.

Data supported the hypothesis that indigenous forbs resist invasion by *C. maculosa* better than grasses because the absence of functionally similar groups was related to the higher *C. maculosa* densities and biomass. These results suggest the degree of functional diversity may not be as important in *C. maculosa* invasion as the composition of functional groups in the community (Symstad 2000, Diaz and Cabido 2001, Tilman et al. 2001) because competition may be more active within functionally similar groups (Lavorel et al. 1999). The proposed mechanism for invasion resistance by morphologically similar indigenous and nonindigenous forbs is that they share physiological traits and ecosystem function (Johnson 1985, Smith et al. 1998). The presence of indigenous forbs increases the degree of interspecific resource competition with a nonindigenous invader and may inhibit their recruitment success (Brown 1998, Symstad 2000, Dukes 2001, Carpinelli 2001). On site 1, removing nothing, spikemoss, shallow-rooted forbs, deep-rooted forbs, or grasses singularly resulted in low *C. maculosa* densities and biomass. Limited *C.*

maculosa invasions into these treatments may be a response of relatively diverse plots with functional groups present that share close traits to the invader. *Centaurea maculosa* density and biomass increased when all forbs were removed from either site. Removing all forbs opened complementary niches to the grass vegetation in the community that may have allowed greater resource acquisition by *C. maculosa* (Hooper and Vitousek 1997) and a higher likelihood of establishment in the grass monocultures (Dukes 2001).

Seasonal variations in *C. maculosa* density followed a bell-shaped curve for most treatments. *Centaurea maculosa* density increased from spring to summer on all treatments except the control and where all plant material was removed. The increase in *C. maculosa* may be due to late spring moisture increasing nutrient gain through mass flow. In most treatments, *C. maculosa* seedlings died by mid-summer perhaps due to increased competition for resources from diverse functional groups (Brown 1998, Symstad 2000, Carpinelli 2001, Dukes 2001). On plots where all vegetation was removed, seedlings survived into the fall. The lower degree of competition for resources such as light, water, and nutrients may have contributed to their survival. This treatment also had higher levels of soil nutrients (Chapter 4) available to the rapid growing *C. maculosa*. *Centaurea maculosa* density on plots where all forbs were removed did not decrease from summer to fall on site 2. The removal of functionally similar indigenous groups may have increased resource availability and decreased competition allowing *C. maculosa* to persist (Hooper and Vitousek 1997, Symstad 2000, Dukes 2001).

Functional group diversity and composition was important for resisting invasion in our research but species diversity within a functional group was also important because it

added to ecosystem complexity, increased productivity and may have contributed to a preemption of resources (Case 1990, Lavorel et al. 1999, Tilman 2001). Species diversity within a functional group may fill a more subtle temporal and spatial niche than functional group diversity alone (Prieur-Richard and Lavorel 2000), making each type of diversity appropriate at different scales (Walker 1992). Individual species diversity within a functional group may be redundant in that they have the same general ecological role (Smith et al. 1998, Diaz and Cabido 2001). However, because species within a group differed in traits and range of environmental tolerance, greater species diversity within a functional group increased the likelihood of containing a species that will thrive in the community under different conditions (Tilman 1994). Our sites had high representation of phenologically different species within a functional group which may have increased the level of competition with *C. maculosa* throughout the growing season and in varying conditions. Enhanced species diversity within a functional group also increases the likelihood particular key species are present which may have an increased ability to resist invasion (McGrady-Steed et al. 1997). The absence of the key species can be more important the ecosystem processes than the presence of another in large quantity (Holling 1992, Sala et al. 1996 Power et al. 1996). In this study, *Liatris punctata* (Hook) was one of the only indigenous forbs with the same phenology as *C. maculosa*. It is possible this species alone competes more with *C. maculosa* for resources than all other forbs.

Plant functional groups, assigned according to the form and function of the vegetation, provide a link between the physiological and life history strategies at the plant level and the processes at the ecosystem level (Chapin 1993). If we assume that species

within a functional group have the same ecological role, then it is logical to believe indigenous and nonindigenous plants with similar morphologies have similar ecological roles in the community (Johnson 1985). Our research suggests that indigenous and nonindigenous forbs have similar functional roles because the presence of indigenous forbs precludes the presence of *C. maculosa*, perhaps through resource preemption. Therefore functional group composition is important because a plant community missing a keystone functional group has a greater susceptibility of invasion.

Our study has important management implications for establishing and maintaining weed resistant plant communities. Grasslands higher in functional group diversity are critical for resisting invasion by nonindigenous invaders. The role of various indigenous functional groups, particularly forbs, and their composition in the plant community needs to be considered more seriously in future grassland management. Maintaining functional group diversity should be a primary objective of land managers, because increased functional group diversity correlates with increased stability through niche differentiation and resource acquisition (Tilman 1997, Naeem 1994, Levine and D'Antonio 1999, Tilman et al. 2001, Anderson and Inouye 2001, Symstad 2000, Dukes 2001). Indigenous forb functional groups may use resources similarly to *C. maculosa* and were a critical component in invasion resistance. The goal of invasive plant management must be to establish and maintain these keystone functional groups.

References

- Anderson, J.E., and R.S. Inouye 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological Monographs* 71(2): 531-556.
- AOSA. 2000. Rules for testing seeds Association of Official Seed Analysis, Lincoln, Nebraska.
- Brown, C. S. 1998. Restoration of California Central Valley grasslands: applied and theoretical approaches to understanding interactions among prairie species. Thesis (Ph.D.) University of California, Davis, California.
- Burke, M. J., and J.P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* 77(3): 776-790.
- Callaway, R. M., and E. T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290: 521-523.
- Carpinelli, M. F. 2001. Designing weed-resistant plant communities by maximizing niche occupation and resource capture. Thesis (Ph.D.) Montana State University, Bozeman, Montana.
- Case, T. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Ecology* 87: 9610-9614.
- Chapin, F. S. I. 1993. Functional role of growth forms in ecosystem and global processes. *In: Scaling Physiological Processes: Leaf to Globe*. J.R Ehleringer and C.B. Field (eds.) Academic Press. San Diego, California.
- Christian, J. M., and S.D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the northern great plains. *Ecology* 80(7): 2397-2407.
- Cronquist, A., A. H. Holmgren, N. H. Holmgren, J. L. Reveal, and P. K. Holmgren. 1977. *Intermountain Flora; Vascular Plants of the Intermountain West, U.S.A.* Columbia University Press, New York, New York.
- Darwin, C. 1859. *The Origin of Species*. Reprinted by Penguin Books, London, UK.
- Davis, M.A., and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. *Ecology Letters* 4: 421-428.

- Diaz, S., and M. Cabido. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16(11): 646-655.
- Dorn, R. D. 1984. *Vascular Plants of Montana*. Mountain West Publishers, Cheyenne, Wyoming.
- Dukes, J. 2001. Biodiversity and invasibility in grassland microcosms. *Oecologia*. 126: 563-568.
- Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. The University of Chicago Press, Chicago, Illinois.
- Goelz, J. C. G. 2001. Systematic experimental designs for mixed species plantings. *Native Plants Journal* 2(1): 90-96.
- Goodman, D. 1975. The theory of diversity-stability relationships in ecology. *The Quarterly Review of Biology* 50(3): 237-267.
- Hakim, S. E. A. 1979. Range condition of the Threemile game range in western Montana. Thesis (M. S.) University of Montana, Missoula, Montana.
- Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecological monographs* 62(4): 447-502.
- Hooper, D. U. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology* 79(2): 704-719.
- Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Nature* 277: 1302-1305.
- Jacobs, J. S. and R.L. Sheley. 1998. Observation: life history of spotted knapweed. *Range Management* 51(6): 665-673.
- Johnson, H. B. 1985. Consequences of species introductions and removals on ecosystem function- implications for applied ecology. *In* Proc. Int. Symp. Biol. Contr. Weeds. E. S. Delfosse (ed.) Vancouver, British Columbia.
- Kedzie-Webb, S. A., R.L. Sheley, J.J. Borkowski, and J.S. Jacobs. 2001. Relationships between *Centaurea maculosa* and indigenous plant assemblages. *Western North American Naturalist*. 61(1): 43-49.

- Kurtz, G. L., R. A. Olson, and T. D. Whitson. 1995. Ecological impacts of Russian knapweed (*Centaurea repens* L.) infestations: small mammal and habitat associations. *In* Proc. West. Soc. Weed Sci., vol. 56.
- Lacey, R. L., C. B. Marlow, and J. R. Lane. 1989. Influence of spotted knapweed (*Centaurea maculosa*) on surface runoff and sediment yield. *Weed Technology* 3: 627-631.
- Lauenroth, W. K., J. L. Dodd, and P. L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia* 36: 211-222.
- Lavorel, S., A. H. Prieur-Richard, and K. Grigulis. 1999. Invasibility and diversity of plant communities: from patterns to processes. *Diversity and Distributions* 5: 41-49.
- Lawton, J. H., and V.K. Brown. 1993. Redundancy in Ecosystem. *In* Biodiversity and Ecosystem Function. E. D. Schulze, and H.A. Mooney (eds.), pp. 255-270. Springer-Verlag, New York, New York.
- LeJeune, K. D., and T. R. Seastedt. 2001. *Centaurea* species: the forb that won the west. *Conservation Biology* 15(6): 1568-1574.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of the evidence linking diversity and invasibility. *Oikos* 87: 15-26.
- Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13(5): 195-198.
- MacArthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- McGrady-Steed, J., P. M. Harris, and P. J. Morin. 1997. Biodiversity regulates ecosystem predictability. *Nature* 390: 162-165.
- Mueggler, W. F., and W. L. Stewart. 1980. *Grassland and Shrubland Habitat Types of Western Montana*. Intermountain Forest and Range Experimental Station, Ogden, Utah.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. W. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734-737.

- Olson, B. E. 1999. Impacts of noxious weeds on ecological and economic systems. *In* The Biology and Management of Noxious Rangeland Weeds. R. L. Sheley and J. K. Petroff (eds.), pp. 4-18. Oregon State University Press, Corvallis, Oregon.
- Orians, G. H. 1984. Site characteristics favoring invasion. *In* Ecology of Biological Invasions in North America and Hawaii. H. A. Mooney and J. A. Drake (eds.) Springer-Verlag, New York, New York.
- Pimm, S. L. 1991. The balance of nature? University of Chicago Press, Chicago, Illinois.
- Pokorny, M. L., J. S. Jacobs, and R. L. Sheley. 2001. Prescribed fire effects on Dalmatian toadflax. *In* Proc. Society for Range Management 54th Annual Meeting, Kailua-Kona, Hawaii.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience* 46(8):609-620.
- Prieur-Richard, A. H., and A. Lavorel. 2000. Invasions: the perspective of diverse plant communities. *Austral Ecology* 25: 1-7.
- Rejmanek, M. 1996. A theory of seed plant invasiveness: the first sketch. *Biological Conservation* 78: 171-181.
- Rejmanek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? *Ecology* 77(6):1655-1661.
- Robinson, G. R., J. F. Quinn, and M. L. Stanton. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* 76(3): 786-794.
- Roy, J. 1990. In search of the characteristics of plant invaders. *In* Biological Invasions in Europe and the Mediterranean Basin. F. di Castri, A. J. Hansen, and M. Debussche (eds.). Kluwer Academic Publishers, Dordrecht, Netherlands.
- SAS Institute Inc. 1990. SAS/STAT Users Guide. Version 6, volume 2. Cary, North Carolina.
- Sakai, A. K., F. K. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. *Annu. Rev. Ecol. Syst.* 32:305-332.

- Sala, O. E., W. K. Lauenroth, S. J. McNaughton, G. Rusch, and X. Zhang. 1996. Biodiversity and ecosystem function in grasslands. John Wiley & Sons, Chichester, Massachusetts.
- Sheley, R. L., and J. K. Petroff (eds.). 1999. The Biology and Management of Noxious Rangeland Weeds. Oregon State University Press, Corvallis, Oregon.
- Sheley, R. L., J. S. Jacobs, and M. F. Carpinelli. 1998. Disturbance, biology, and management of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). Weed Technology. 12:353-362.
- Sheley, R. L., B. E. Olson, and L. L. Larson. 1997. Effect of weed seed rate and grass defoliation level on diffuse knapweed. Range Management 50(1): 39-43.
- Sheley, R. L., T. J. Svejcar, and B. D. Maxwell. 1996. A theoretical framework for developing successional weed management strategies on rangeland. Weed Technology 10: 766-773.
- Smith, T. M., H. H. Shugart, and F. I. Woodward. 1998. Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change. Cambridge University Press, Cambridge, UK.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69(1): 25-46.
- Symstad, A. J. 2000. A test of the effects of functional group richness and composition on grassland invasibility. Ecology 81(1): 99-109.
- Symstad, A. J., and D. Tilman. 2001. Diversity loss, recruitment limitation, and ecosystem functioning: lessons learned from a removal treatment. Oikos 92: 424-435.
- Tilman, D. 1993. Community diversity and succession: the roles of competition, dispersal, and habitat modification. In Biodiversity and Ecosystem Function. E. D. Schulze, and H. A. Mooney (eds.), pp. 328-343. Springer-Verlag, New York, New York.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75(1): 2-16.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379: 718-720.

- Tilman, D. 1997a. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78(1): 81-92.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie and E. Siemann. 1997b. The influence of functional diversity and composition on ecosystem process. *Science* 277: 1300-1305.
- Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. *Science* 294(26): 843-845.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, J. M. Melillo. 1997. Human domination of earth's ecosystems. *Science* 277: 494-499.
- Walker, B. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6(1): 18-23.
- Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* 75(1):151-165.
- Zar, J. H. 1999. *Biostatistical Analysis*, 4 edition. Prentice Hall, Upper Saddle River, New Jersey.

CHAPTER 4

ECOLOGICAL ROLE OF INDIGENOUS FUNCTIONAL
AND A NONINDIGENOUS INVADER IN A
GRASSLAND PLANT COMMUNITYIntroduction

During the past century, ecologists have described the structure of major grassland vegetation types of western North America (Clements 1920, Stoddart and Smith 1943, Daubenmire 1970, Mueggler and Stewart 1980). To date, little is known about the role, or function, of species, or groups of species, occurring within grasslands. Most of that known emphasizes grasses over other functional groups (White 1973, Mueggler and Stewart 1980, Holechek et al. 1989, Sheaffer et al 1992). Furthermore, little is known about plant function and ecosystem processes as functional group diversity changes. By definition, species within functional groups share physiological and morphological traits and provide similar roles in the ecosystem (Lauenroth et al. 1978, Chapin 1993). Ecological roles can be partially defined by nutrient and water cycles which provide a mechanistic understanding of plant community structure, dynamics, and trajectories (Daubenmire 1970, Tilman 1988, McJannet et al. 1995). Research implies indigenous functional groups evolved to fill selected ecological roles because they differ in nutrient accumulation, storage, conservation strategies, and concentration (Parriah and Bazzaz 1976, McJannet et al. 1995, Carrera et al. 2000, Duke and Caldwell 2001, Reich et al. 2001). Functional groups may be utilizing soil nutrients and water from separate temporal

and spatial niches (Parriah and Bazzaz 1976, Berendse 1979, McKane et al. 1990, Golluscio and Sala 1993). Altering plant functional group diversity and composition may influence the primary productivity, nutrient cycling, and water cycling within the community (Hooper and Vitousek 1997, Tilman 1997, Dukes 2001, Peltzer and Kochy 2001). Understanding the ecological role of various indigenous functional groups is important because it provides basic information about plant community dynamics. It also provides baseline information necessary for developing restoration goals, assessing the effects of management, and directing plant communities to a desired state (Lauenroth et al. 1978, Pickett et al. 1987, McLendon and Redente 1991, Sheley et al. 1996, Tilman et al. 1999).

While little is known about the ecological role of indigenous functional groups, even less is known about the ecological role of nonindigenous invaders. Some studies suggest indigenous and nonindigenous plants may have similar ecological roles (Johnson 1985, Thompson et al. 1995, Reich et al. 2001) while others disagree (Risser 1994, Vitousek 1990, LeJeune and Seastedt 2001). The degree of similarity could have profound implications on the ecological risk associated with their invasion. It is often stated that nonindigenous plants alter the function of indigenous plant communities (Lacey et al. 1989, Mack and D'Antonio 1998, Sheley et al. 1998, Olson 1999). Evidence of a nonindigenous invader's effect on an indigenous plant community is often contradictory, even when examining the same species in western North American grasslands. For example, the nonindigenous grass *Bromus tectorum* has been found to alter nutrient dynamics in some studies (Evans et al. 2001) but not in others (Svejcar and Sheley 2001).

Other evidence suggests nonindigenous invaders may reduce soil nutrient availability (Christian and Wilson 1999), possibly by having higher nutrient uptake rates and increasing the rate of nutrient cycling (Vinton and Burke 1995). Alternatively, Ehrenfeld et al. (2001) suggested a nonindigenous invader promoted increases in nutrient availability. Mack et al. (2001) indicate that nonindigenous invaders affect nutrient cycles indirectly by altering disturbance regimes such as fire. Many ecological impacts associated with nonindigenous plant invasions are hypothesized but not well understood (D'Antonio and Vitousek 1992). Few studies are designed to elucidate nonindigenous species as causal factors. Understanding the ecological roles and impacts of nonindigenous invaders on plant community function is critical for developing invasive plant management strategies because it provides information necessary for ecological risk assessment.

Susceptibility of western North America grasslands to invasion may be influenced by community structure (Oriens 1984), resource availability (Elton 1958, Burke and Grime 1996, Tilman et al. 1996, Stoltgren et al. 1999) and invader traits (Davis and Pelsor 2001). Emerging theories of invasion resistance are mechanistically linked to nutrient availability. A number of researchers have suggested that functionally diverse plant assemblages resist invasion (Elton 1958, Burke and Grime 1996, Levine and D'Antonio 1999) through resource preemption (Tilman 1999, Symstad 2000, Davis and Pelsor 2001, Dukes 2001). Niche differentiation is the suggested mechanism for resource depletion found in experiments and theory (Naeem et al. 1994, Tilman et al. 1996 and 1997, Hooper and Vitousek 1997, Hooper 1998), and maximizing niche occupation has been shown to decrease community invasibility (Brown 1998, Carpinelli 2001). Another mechanistic-

based invasion theory is the fluctuating resource availability hypothesis, which implies that plant communities are more susceptible to invasion under conditions of increased unused resources (Hobbs and Atkin 1988, Maron and Connors 1996, Burke and Grime 1998, Davis et al. 2000). Therefore, a community's susceptibility to invasion fluctuates temporally and can be determined by a limiting resource. Even short-term increases in resource availability can temporarily reduce or suspend competition intensity, and in turn, invasion (McNaughton 1993, Davis and Pelsor 2001). Research clarifying invasion mechanisms is needed (Lavorel et al. 1999, Prieur-Richard and Lavorel 2000), because support of these hypotheses is confounding and incomplete. For example, empirical evidence suggesting diverse communities resist invasion has not considered factors such as disturbance and fertility (Prieur-Richard and Lavorel 2000). This is also the case with research suggesting community diversity increases invasion (Robinson et al. 1995, Rejmanek 1996, Smith and Knapp 1999, Stohlgren et al. 1999). In these examples, favorable biotic or abiotic conditions, including nutrient and water availability, co-vary with diversity.

There is a need for studies addressing invasion mechanisms of the invaded community, and invader success in communities with different levels of functional diversity (Lavorel et al. 1999). Understanding the influence of nonindigenous plants on ecosystem function is critical for ecologically-based invasive plant management. This knowledge could lead to management strategies that modify processes directing plant community changes rather than managing a symptom of a problem (Pickett et al. 1987, Sheley et al. 1996, Ehrenfeld and Toth 1997). Without a predictive understanding of the

influence of management on ecosystem function, the decision to impose a particular strategy is arbitrary, and the consequences are unknown.

In this research, we quantified portions of the nutrient and hydrologic cycles of several functional groups. We also compare the basic ecological functions between indigenous functional groups and a nonindigenous invader. Our specific objectives were to quantify the nitrogen (N), phosphorus (P), potassium (K), sulfur (S), carbon (C), and water cycles of the following indigenous functional groups: shallow-rooted forbs, deep-rooted forbs, grasses, spikemoss, and a nonindigenous invader, *Centaurea maculosa* (spotted knapweed). More specifically, we quantified the total N, nitrate ($\text{NO}_3\text{-N}$), ammonium ($\text{NH}_4\text{-N}$), P, K, S, total C, and water cycles in the soil and the concentration (percent) and uptake (concentration x biomass) of N, P, K, and S in aboveground plant tissue. We hypothesized that indigenous functional groups have different ecological roles, and that removing a functional group, singularly or in concert, would alter the soil nutrient and hydrologic cycles, with the impact increasing with removal intensity. We also hypothesized indigenous and nonindigenous forbs have similar ecological roles cycling N, P, K, and S in plant tissue because they share morphological, and perhaps, physiological traits. Because nonindigenous invaders are thought to impact ecosystem processes, we hypothesized that *C. maculosa* would alter nutrient and water cycles in the soil, and that the presence of *C. maculosa* would alter the ability of indigenous functional groups to capture resources. Although we focus on one nonindigenous species in this research, other deep-rooted nonindigenous forbs may act similarly.

Methods

Study sites

This study was conducted on two sites within the *Festuca idahoensis*/*Agropyron spicatum* (Idaho fescue/bluebunch wheatgrass) habitat type (Mueggler and Stewart 1980). This habitat type lies at the cool-wet end of grassland habitat types and is widely distributed throughout the mountain grasslands in southwestern Montana and the western United States, providing an excellent model for applied ecological research. Besides the perennial grasses *Festuca idahoensis* Elmer and *Agropyron spicatum* Pursh., predominant indigenous forbs include *Artemisia ludoviciana* Nutt. (prairie sage), *Balsamorhiza sagittata* Nutt. (arrowleaf balsamroot), and *Lupinus* spp. (Lupine), although the proportion of forbs varies with location for this habitat type (Mueggler and Stewart 1980). We chose this grassland habitat type because it is characterized by a high species diversity and is often invaded by *C. maculosa*, and therefore provides an excellent model system for testing the ecological role of indigenous functional groups and a nonindigenous invader in a grassland ecosystem.

Sites were located on the Flying D Ranch approximately 70 km east ($45^{\circ}34' \text{ N}$, $111^{\circ} 34' \text{ W}$) of Bozeman, Montana. Sites lie on an east-northeast aspect of a 20 degree slope at 1,624 m elevation. Prior to plot establishment, soils were tested for the presence of picloram (4-amino-3,5,6-trichloropicolinic acid, potassium salt) to minimize the risk that site characteristics and plant community composition were influenced by recent herbicide applications. Picloram was not detected at the 0.01 mg/kg level. Annual

average precipitation is 41 cm, with peaks in the spring and fall. Annual average temperature ranges from 5.5 to 7°C.

Soil classifications indicated site 1 soils are a loamy-skeletal, mixed, frigid, active Typic Haplocryolls (Haplo Cryic Mollisol). Site 2 soils are a coarse-loamy, mixed, frigid, active Typic Haplocryolls (Haplo Cryic Mollisol). Soil profile descriptions for each site showed small variations in the structure, material and pH of the A and Bw horizons. Main differences in the soil profiles were depth of the A horizon (22 verses 12 cm, site 1 and 2, respectively) and the presence of a Bw horizon at site 2. The Bw horizon structure, which contributed substantially to total profile depth, had larger, blockier soil aggregates (peds) than the A or Bk horizons of each site.

The area has been grazed for decades, and in some years it has been heavily grazed, by either cattle or bison (*Bison bison*) in its recent history (50-60 years). Bison grazing during the past ten years has been sporadic. Windblown slopes are prime winter habitat for wildlife. In the study area, winter use by elk (*Cervus elaphus*) has steadily increased as herd size increased during the past 20 years. In 2000, each site was fenced with a 2 meter, eight strand fence to prevent grazing by livestock and wildlife.

Experimental design

Species of grass, forbs and spikemoss were combined into functional groups based on morphological and physiological similarities. Forbs were divided into two functional groups based on average rooting depth of the species. Prior to removing any species, all forbs were carefully excavated and their root structure and rooting depth determined.

This information was used to determine functional group associations. The distinction between a shallow and a deep depth was based on a natural break within the forb roots sampled which occurred at 15 cm. In cases where the average rooting depth was close to 15 cm, the root type (taproot versus fibrous root) was used to determine which area of the soil the plant was most likely extracting the majority of nutrients and water. For example, species with primarily fibrous roots were considered shallow-rooted while tap-roots were grouped with deep-rooted forbs. The nonindigenous species, *Centaurea maculosa*, is a late-season, deep-rooted forb from Eurasia (Sheley et al. 1998) and was considered its own functional group.

Treatments, arranged in a randomized-complete-block design, were applied by removing one or more functional groups from 2 x 2 m plots. The experiment was a complete factorial design, with 7 removal treatments, 2 nonindigenous invader treatments, 2 sites, and 4 blocks, for a total of 112 plots. The seven removal treatments included removal of: 1) nothing (control), 2) moss, lichens and fern allies (collectively referred to as spikemoss throughout the paper), 3) shallow-rooted forbs, 4) deep-rooted forbs, 5) all grasses, 6) all forbs, and 7) all plant material. The two nonindigenous invader treatments were 1) *C. maculosa* absent and 2) *C. maculosa* present. Removal treatments were applied in the spring of 2000 and maintained biweekly throughout the 2000 and 2001 growing seasons.

Functional groups were removed by carefully brushing a 6% glyphosate [N-(phosphonomethyl) glycine] solution on foliage of target species, minimizing disturbance to surrounding soil and plant community. After plants died, the remaining aboveground

plant material was clipped at ground level and removed from the plot to minimize nutrient leaching from plants to soil. We chose plant removals over additions because experimental removals is the most convincing way of determining interaction strengths (Wootton 1994) and inter-taxa competition (Goelz 2001), and because of the time required to establish mature plant communities.

During September and October 2000, the nonindigenous invader treatments were applied by seeding *C. maculosa* on one-half the plots. *Centaurea maculosa* seeds were collected in August 2000 from Plains, Montana (47°28' N, 114° 53' W). Prior to seeding, seeds were cleaned of insects, vegetative material, and other seeds using a South Dakota Seed Blower (Hoffman Manufacturing Company). Seed germination and viability rate (AOSA 2000) were 55% and 94%, respectively. *Centaurea maculosa* seeds were broadcast biweekly from September 19 to October 31 to mimic natural seedrain (Sheley et al. 1997). Seeding rate, based on the life-history study of Jacobs and Sheley (1998) and Sheley et al. (1997), totaled 2,000 seeds m⁻², or 8,000 seeds per plot.

Sampling and data collection

Soils samples were collected from each plot with a 2.2 cm soil core during the spring, summer, and fall 2001. Spring sampling occurred when the majority of the spring ephemeral forbs were in bloom, summer sampling coincided with peak standing crop, and fall sampling occurred after 95% of the vegetation was senescent. Plots were divided into three subplots which were randomly assigned to either of the spring, summer, or fall sample period during 2001. Within each subplot, three randomly located soil cores were

collected and separated into two depths. Soil samples were taken to coincide with the shallow-rooted (0-15 cm) and deep-rooted (15-40 cm) forbs rooting depths. To capture heterogeneity of soil properties at each season, three samples per depth were collected from each plot and were combined into one sample per plot for analysis. Soils were analyzed for mass water content, total nitrogen (N), nitrate ($\text{NO}_3\text{-N}$), ammonium ($\text{NH}_4\text{-N}$), sulfur (S), phosphorus (P), potassium (K), and total carbon (C) levels. Soil samples collected from the field were weighed, dried (40°C , 160 hours) to a constant weight, weighed again, then ground to pass through a 2 mm sieve. Inorganic soil N ($\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$) was determined on 1 M KCl extracts of soils (5 g soil:50 ml extractant) (Mulvaney 1996) and total N was determined using the Kjeldahl (TKN) method (Bremner 1996). Available P in the soil was measured by the NaHCO_3 extraction method (Olsen et al. 1954). Available K and S were determined by extraction with 1 M NH_4OAc (Helmke and Sparks 1996) and 0.001 M CaCl_2 (Hamm et al. 1973), respectively, using a 5:1 extractant to soil ratio. Filtered extracts were analyzed for P, K, and S by inductively coupled plasma membrane spectroscopy (Jones 1977). Total C was determined by loss-on-ignition (Nelson and Sommers 1996). Gravimetric mass water content was calculated for each soil sample (Brady and Weil 1999).

Centaurea maculosa density was counted in the spring, summer, and fall of 2001 for the entire 2 x 2 meter plot. Biomass of each functional group was collected within three 0.2 x 0.5 m frames, randomly located within the subplots at each sampling period. *Centaurea maculosa* biomass was collected only in the fall of 2001 because it was still establishing during the spring and summer, and harvesting would have affected seedling

establishment. All above-ground current-year growth was harvested at ground level by functional group. Spikemoss biomass was removed as part of the treatments and was not removed in subplots. Plant material was dried (40 ° C, 160 hours) to a constant weight and biomass recorded. Plant tissue was ground and analyzed for nitrogen (N), phosphorus (P), potassium (K), and sulfur (S). Plant tissue analysis for S content was conducted in the spring and fall only. Chemical analysis of plant tissue for total N and S were performed using the Leco CNS-2000 dry combustion analyzer (LECO Corporation). Plant P and K analyses was performed by dry ashing subsamples of the ground plant material according to the procedure described by Jones and Case (1990). Potassium and P concentrations in the dissolved ash were determined using inductively coupled plasma (ICP) membrane spectroscopy (Jones 1977). Nutrient uptake by functional group was determined by multiplying biomass of a functional group by its nutrient concentrations.

Data Analysis

For all analyses, sites were analyzed separately. For soil analyses, shallow and deep soil depths were analyzed separately. Test results were considered significant at the $\alpha \leq 0.05$ level. For ease of interpretation, non-transformed means are presented in the text and tables with test results for transformed data.

Soil. To test the hypotheses that indigenous functional groups have different roles, and that removing plant functional groups from a grassland community would alter nutrient and water cycles in soils, we compared soil parameters among various removal treatments where *C. maculosa* was absent. A multivariate analysis of variance

(MANOVA) was used to compare soil parameters for each treatment by site and soil depth. MANOVA was chosen over separate analysis of variance tests (ANOVAs) because it reduced the risk of a Type I error (Zar 1999). The model analyzed effects of season, functional group, and season*functional group on soil parameter levels. The error term had 720 degrees of freedom. Data was transformed, to meet the assumption of equality of variance, in consecutive order of square root, natural log, and reciprocal until the model met the assumption of equality of variance. We followed MANOVA's Pillai's trace statistic because it is able to accommodate some deviation from equality of variance (Zar 1999). Mean separations were achieved using Tukey post hoc tests (Zar 1999) in SPSS (SPSS 1999).

To determine whether the nonindigenous invader altered nutrient and water cycles in the presence of various combinations of functional groups and/or alone, we included all plots with and without *C. maculosa*. MANCOVA repeated contrasts were used to compare soil parameters of the seven removal treatments in the presence and absence of *C. maculosa*. Because MANCOVA requires the correlation between two variables to be the same across all groups, we used the density of *C. maculosa* (m^2) as a covariate among treatments (Hair et al. 1995). The model was the same as the previous soil analysis. Data was transformed as necessary when predicted versus residual plots indicated the assumption of equal variance had been violated. The *p*-value of the contrast was used to determine significant differences in soil parameters between the presence and absence of *C. maculosa*.

Plant. To test our hypothesis that indigenous and nonindigenous forbs have similar ecological roles, it was important to quantify the nutrient concentration in plant tissue across groups and the mean nutrient uptake by functional group per unit area. Separate ANOVAs were conducted for each of the 4 nutrients. For all ANOVA's, functional group and season were main effects and functional group*season was the interaction term. Indigenous functional group nutrient data was included in the model if the group was grown in the absence of *C. maculosa*. *Centaurea maculosa* plant tissue data was included in the model if it was grown in a monoculture. For plant tissue nutrient concentration, ANOVA was used to compare nutrient concentrations of five nutrients among the five functional groups; grasses, shallow-rooted forbs, deep-rooted forbs, spikemoss and *C. maculosa*. ANOVAs for plant nutrient uptake of N, P, K, and S compared grasses, shallow-rooted forbs, deep-rooted forbs, and *C. maculosa*. Spikemoss was not sampled on a unit area basis; therefore, the percent uptake could not be compared to that of other groups. Data was transformed as necessary when predicted versus residual plots indicated the assumption of equal variance had been violated. Tukey post hoc tests were used to elucidate differences in significant main and interaction effects (SAS 1990).

To determine whether *C. maculosa* altered nutrient percentage and accumulation of indigenous functional groups, we compared the plant nutrient concentration and plant nutrient uptake of grasses, shallow-rooted forbs, deep-rooted forbs and spikemoss growing in the presence and absence of *C. maculosa*. ANCOVA was used for each of the four nutrient parameters; N, P, K, and S. Data was transformed when necessary to meet assumptions of equality of variance. *Centaurea maculosa* density was used as the

covariate. Functional group and season were the main effects and functional group*season was the interaction term. Contrast *p*-values determined differences in plant nutrient concentration and plant nutrient uptake between vegetation grown in the presence and absence of *C. maculosa*.

Results

Ecological role of functional groups in nutrient and hydrologic cycles

Seasonal soil nutrient variations. **Site 1.** Soil nutrient and water parameters depended on the season and removal treatment main effects for both sites and soil depths, but were not dependent on the interaction of season and removal treatment in any case (Table 4.1). Therefore, in text and tables, mean seasonal soil nutrient values are averaged over removal treatments, and means removal treatment soil nutrient values are averaged over seasons. Fall values for NO₃-N, NH₄-N, P, and S were at least one-third their spring levels. Total soil C and N for both depths decreased slightly from spring to fall at this site. By fall, soil water decreased at both soil depths, but rose slightly in summer in the deep soil depth before declining in the fall. Plant available K in the soil remained constant across seasons. Deep soil strata had lower values for all soil parameters than the shallow soil strata, except for soil water content and NH₄-N. (Data not shown.)

Site 2. In the shallow soil depth at site 2, values for total N, NO₃-N, NH₄-N, K, S, and total C did not differ across seasons. Soil parameters which remained relatively constant in the deep depth from spring to fall were total N, NO₃-N, K, and S. The level of NH₄-N in the deep soil depth decreased from spring to fall. Phosphorus levels in both soil

depths decrease by about one-half from spring to fall. By fall, soil water decreased by one-half its spring value in the shallow soil depth and one third its spring value in the deep soil depth. Total soil C increased from spring to fall. Most soil parameter levels had lower values in the deep soil strata compared to shallow soil strata. The exception was soil water at site 2. (Data not shown.)

Table 4.1. Pillai's trace MANOVA statistic results for total N, NO₃-N, NH₄-N, P, K, S, total C and soil water content at sites 1 and 2 shallow and deep soil depths. Error term has 576 degrees of freedom.

Site	Soil Depth (cm)	Source	df	F	P-value
1	Shallow (0-15)	SEASON	16	22.1	<0.0001
		TREATMENT	56	1.6	0.008
		SEASON*TREATMENT	112	0.8	0.951
1	Deep (15-40)	SEASON	16	20.5	<0.0001
		TREATMENT	56	1.6	0.006
		SEASON*TREATMENT	112	0.9	0.737
2	Shallow (0-15)	SEASON	16	13.0	<0.0001
		TREATMENT	56	2.2	<0.0001
		SEASON*TREATMENT	112	1.1	0.271
2	Deep (15-40)	SEASON	16	5.2	<0.0001
		TREATMENT	56	1.6	0.004
		SEASON*TREATMENT	112	1.0	0.490

Soil nutrients response to removal treatments. **Site 1 shallow soil depth.** Soil NO₃-N was nearly three times higher in treatments where all vegetation was removed, either with or without *C. maculosa*, than in any other treatment (Table 4.2). Soils from the control had less NH₄-N than soils where all vegetation was removed. All other

treatments had similar $\text{NH}_4\text{-N}$ levels, averaging 8.0 mg/kg. Phosphorus levels were 1.5 times higher where all plant material was removed than where spikemoss or deep-rooted forbs were removed. All other treatments yielded similar soil P. Values of total N, K, S, total C, and soil water did not differ among removal treatments.

Site 1 deep soil depth. Nitrate was the only soil parameter to differ among treatments in site 1 deep soil strata (Table 4.3). Treatments where nothing, spikemoss, or deep-rooted forbs were removed had the lowest $\text{NO}_3\text{-N}$ levels, averaging 3.6 mg/kg. When grasses or all forbs were removed, $\text{NO}_3\text{-N}$ levels were similar and slightly higher than the control. Removing all plant material and adding *C. maculosa* produced a $\text{NO}_3\text{-N}$ level of 7.92 mg/kg. This level was similar to soil $\text{NO}_3\text{-N}$ levels where grasses, all forbs, or all vegetation was removed but higher than $\text{NO}_3\text{-N}$ levels of the control. When all vegetation was removed, the $\text{NO}_3\text{-N}$ level was 8.5 mg/kg. Removing shallow-rooted forbs created $\text{NO}_3\text{-N}$ levels similar to all other treatments.

Site 2 shallow soil depth. Removing functional groups did not influence soil nutrient levels of total N, K, S, and total C in site 2 shallow soil strata (Table 4.4). Means for these soil parameters were 0.3%, 324 mg/kg, 7.3 mg/kg, and 3.3%, respectively. Nitrate was highest in soils where all plant material was removed, in the presence (8.3 $\text{NO}_3\text{-N}$ mg/kg) and absence (9.2 $\text{NO}_3\text{-N}$ mg/kg) of *C. maculosa*. All other removal treatments raised soil $\text{NO}_3\text{-N}$ over that of the control, which was 1.5 mg/kg, but below that of complete vegetation removals. Soil $\text{NH}_4\text{-N}$ increased over the control where one or more functional groups were removed. Removing grasses, or all vegetation, in the presence or absence of *C. maculosa*, tended to have the highest $\text{NH}_4\text{-N}$ levels, averaging

Table 4.2. Removal treatments' mean soil parameters ,averaged over seasons, for site 1 shallow soils depth (0-15 cm). Removal treatments were initiated in the spring of 2000, and soil parameters measured spring, summer, and fall 2001. Values in each column which do not share the same letter are significantly different ($\alpha < 0.05$, MANOVA followed by Tukey post hoc test).

Functional Group Removal Treatments	Soil Parameters							
	Total N (%)	NO ₃ -N (mg/kg) [§]	NH ₄ -N (mg/kg) [†]	P (mg/kg)	K (mg/kg)	S (mg/kg)	Total C (%)	Water Content (kg/kg)
Control	0.34	3.1a	8.3a [‡]	4.5ab	333	8.9	3.6	0.097
Spikemoss	0.37	2.5a	6.6ab	4.3a	351	8.2	3.6	0.088
Shallow Forbs	0.39	3.7a	7.9ab	4.6ab	344	7.7	3.6	0.090
Deep Forbs	0.34	3.3a	7.7ab	4.0a	350	7.6	3.3	0.099
Grass	0.35	5.0a	9.0ab	4.9ab	337	8.1	3.4	0.088
All Forbs	0.34	4.1a	8.5ab	4.7ab	341	8.4	3.4	0.098
All Plant Material	0.36	10.9b	10.7b	6.4b	353	8.6	3.7	0.097
All Plant Material, with <i>C. maculosa</i> added	0.35	8.2b	7.7ab	5.8ab	337	7.2	3.6	0.110

[§] Test results for the column represent the natural log transformation but non-transformed means are presented.

[†] Test results for the column represent the reciprocal transformation but non-transformed means are presented.

[‡] An extreme values exists in the data set. The outliers raised the mean NH₄-H value of the Control to appear similar to other treatment means. The test results indicate the Control has a lower NH₄-H level than when all plant material is removed, and it does when the outlier is removed. With the outlier removed, the NH₄-H mean for the Control is 5.56mg/kg. Test results were the same with and without the outlier.

Table 4.3. Removal treatments' mean soil parameters ,averaged over seasons, for site 1 deep soil depth (15-40 cm). Removal treatments were initiated in the spring of 2000, and soil parameters measured spring, summer, and fall 2001. Values in each column which do not share the same letter are significantly different ($\alpha < 0.05$, MANOVA followed by Tukey post hoc test).

Functional Group Removal Treatments	Soil Parameters							
	Total N (%)	NO ₃ -N (mg/kg) [§]	NH ₄ -N (mg/kg)	P (mg/kg)	K (mg/kg)	S (mg/kg)	Total C (%)	Water Content (kg/kg)
Control	0.26	3.2a	8.5	3.8	313	6.8	2.7	0.11
Spikemoss	0.26	4.0a	8.3	3.5	347	7.8	2.7	0.09
Shallow Forbs	0.27	6.3abc	11.3	4.1	318	7.4	2.7	0.10
Deep Forbs	0.27	3.8a	9.1	3.8	311	7.1	2.6	0.10
Grass	0.27	4.5ab	8.7	4.2	307	6.8	2.9	0.11
All Forbs	0.25	5.0ab	10.0	4.3	315	8.3	2.8	0.11
All Plant Material	0.28	8.5c	7.7	5.1	345	7.9	3.0	0.13
All Plant Material, with <i>C. maculosa</i> added	0.22	7.9bc	12.1	4.4	305	7.8	2.5	0.11

[§] Test results for the column represent the natural log transformation but non-transformed means are presented.

Table 4.4. Removal treatments' mean soil parameters values, averaged over seasons, for site 2 shallow soil depth (0-15 cm). Removal treatments were initiated in the spring of 2000, and soil parameters measured spring, summer, and fall 2001. Values in each column which do not share the same letter are significantly different ($\alpha < 0.05$, MANOVA followed by Tukey post hoc test).

Functional Group Removal Treatments	Soil Parameters							
	Total N (%)	NO ₃ -N (mg/kg) [§]	NH ₄ -N (mg/kg) [†]	P (mg/kg)	K (mg/kg)	S (mg/kg)	Total C (%)	Water Content (kg/kg) [‡]
Control	0.33	1.5a	5.7a	5.1ab	325	7.2	3.5	0.081a
Spikemoss	0.29	2.1ab	5.9ab	4.9a	348	7.1	3.4	0.087a
Shallow Forbs	0.34	2.7b	7.1abc	4.9a	330	6.8	3.4	0.082a
Deep Forbs	0.28	2.4b	6.9abc	5.7ab	307	6.7	3.3	0.088a
Grass	0.29	3.2b	7.8bcd	4.9a	326	7.6	3.3	0.091ab
All Forbs	0.32	3.5b	7.1abc	6.2ab	323	7.3	3.5	0.083a
All Plant Material	0.29	9.2c	8.5cd	7.3ab	324	7.0	3.1	0.111b
All Plant Material, with <i>C. maculosa</i> added	0.29	8.3c	15.6d	7.6b	312	8.4	3.3	0.093ab

[§] Test results for the column represent the natural log transformation but non-transformed means are presented.

[†] Test results for the column represent the reciprocal transformation but non-transformed means are presented.

[‡] Values for the column represent the square root transformation but non-transformed means are presented.

10.6 mg/kg. All treatments had similar soil P levels, except where all vegetation was removed and *C. maculosa* was seeded. This treatment increased P levels above treatments where spikemoss, shallow-rooted forbs, or grasses were removed. Removing all vegetation increased the soil water content above the level of all removal treatments, except where grasses or all vegetation were removed in the presence of *C. maculosa* seeded.

Site 2 deep soil depth. Removal treatments had no effect on levels of total N, K, S, total C, and mass water content in site 2 deep soils (Table 4.5). Removing all vegetation, either in the presence or absence of *C. maculosa*, increased soil NO₃-N levels about three times above that of all other treatments. All treatments had NH₄-N levels similar to the control, except where all vegetation was removed in the presence or absence of *C. maculosa*. These treatments differed in NH₄-N from the control, but were similar to other treatments. Soils where all vegetation was removed, either with or without *C. maculosa*, had P levels twice as high as soils where all forbs or shallow-rooted forbs were removed. All other treatments had similar P values.

Plant nutrient concentration. Nitrogen. Plant tissue concentration (percent) of N depended on the interaction of functional group and season on both sites (site 1: $F_{6, 218}=68.9, p<0.0001$; site 2: $F_{6, 218}=46.5, p<0.0001$). Therefore, functional group nutrient concentration values presented in the text and table are the seasonal mean of all removal treatments where the group was present. Percent N did not differ between the spikemoss and grass functional groups in the spring and summer at either site (Table 4.6).

Table 4.5. Removal treatments' mean soil parameters values, averaged over seasons, for site 2 deep soil depth (15-40 cm). Removal treatments were initiated in the spring of 2000, and soil parameters measured spring, summer, and fall 2001. Values in each column which do not share the same letter are significantly different ($P < 0.05$, MANOVA followed by Tukey post hoc test).

Functional Group Removal Treatments	Soil Parameters							
	Total N (%)	NO ₃ -N (mg/kg)	NH ₄ -N (mg/kg) [†]	P (mg/kg)	K (mg/kg)	S (mg/kg)	Total C (%)	Water Content (kg/kg) [§]
Control	0.23	2.1a	5.1a	3.8ab	298	7.6	2.5	0.104
Spikemoss	0.20	1.8a	5.7ab	3.5ab	291	6.9	2.3	0.123
Shallow Forbs	0.21	2.5a	5.9ab	2.8a	290	6.0	2.4	0.105
Deep Forbs	0.24	2.8a	6.4abc	4.5ab	293	6.5	2.7	0.100
Grass	0.23	2.5a	6.3abc	3.7ab	298	6.8	2.7	0.224
All Forbs	0.18	2.7a	6.0ab	2.8a	256	7.1	2.2	0.118
All Plant Material	0.22	8.3b	11.6c	5.5b	298	8.9	2.7	0.118
All Plant Material, with <i>C. maculosa</i> added	0.22	8.1b	13.8bc [‡]	5.7b	282	8.9	2.5	0.111

[§] Test results for the column represent the natural log transformation but non-transformed means are presented.

[†] Test results for the column represent the reciprocal transformation but non-transformed means are presented.

[‡] Two extreme values exist in the data set. One of the outliers raised the mean NH₄-H value to appear higher where all plant material was removed and *C. maculosa* added than when in the absence of *C. maculosa*. With the two outliers removed, the mean of all plant material removed was 8.62 and the mean for all plant material removed with *C. maculosa* added was 7.80. Test results were the same with and without the outlier.

Table 4.6. Seasonal variations of mean plant tissue nutrient concentrations within a functional group, and variations in mean plant tissue nutrient concentrations among functional groups. For each functional group, the seasonal nutrient value is averaged over all removal treatments where the functional group was present. Plant biomass was collected in 2001. Values in each column, within a site, which do not share the same letter are significantly different ($\alpha < 0.05$, ANOVA followed by Tukey post hoc test). Significant seasonal differences are discussed in the text.

Site	Functional Group	N	Tissue Nutrient Concentration (%)										
			Nitrogen			Phosphorus			Potassium [§]			Sulfur [†]	
			Spring	Summer	Fall	Spring	Summer	Fall	Spring	Summer	Fall	Spring	Fall
1	Spikemoss	60	1.57a	1.59ab	1.66c	0.14a	0.09a	0.10c	0.27a	0.27a	0.46a	0.14a	0.14bc
	Shallow Forbs	48	2.15b	1.76bc	1.11b	0.22b	0.14b	0.09bc	2.18c	2.05c	1.42c	0.30b	0.13bc
	Deep Forbs	48	2.96c	1.91c	0.89ab	0.28c	0.10a	0.07ab	2.91c	2.04c	1.18c	0.26b	0.12b
	Grass	60	1.75a	1.45a	0.82a	0.16a	0.10a	0.06a	1.23b	1.01b	0.73b	0.15a	0.10a
	<i>C. maculosa</i>	4	n/a	n/a	2.14d	n/a	n/a	0.13c	n/a	n/a	1.39bc	n/a	0.18c
2	Spikemoss	60	1.46a	1.53a	1.59d	0.10a	0.09a	0.10c	0.40a	0.34a	0.34a	0.13a	0.14c
	Shallow Forbs	48	2.30b	1.91b	1.21bc	0.19b	0.14c	0.09bc	2.22c	1.95c	1.52c	0.32b	0.14c
	Deep Forbs	48	2.81c	1.94b	0.98ab	0.21b	0.11b	0.08ab	2.23c	1.75c	1.20c	0.25b	0.12b
	Grass	60	1.58a	1.52a	0.92a	0.11a	0.10ab	0.06a	1.16b	1.00b	0.60b	0.12a	0.08a
	<i>C. maculosa</i>	4	n/a	n/a	1.56cd	n/a	n/a	0.10bc	n/a	n/a	1.74c	n/a	0.13bc

[§] Test results represent the natural log transformation for site 1 and the reciprocal transformation for site 2. Non-transformed means are presented.

[†] Test results for the column represent the square root transformation but non-transformed means are presented.

Shallow-rooted forbs and deep-rooted forbs had high percent N that differed from percent N of spikemoss and grasses on both sites in the spring and summer. In the spring, shallow- and deep-rooted forbs also differed from each other in N concentration, 2.15% and 2.96%, respectively on site 1, and 2.30% and 2.81% respectively at site 2. In the fall, when *C. maculosa* tissue was also analyzed, N concentration was greater in *C. maculosa* than any functional group at site 1. Nitrogen concentration of shallow-rooted forbs was similar to the deep-rooted forbs in the fall on site 1. Deep-rooted forb percent N was also similar to grasses but differed from spikemoss on this site. At site 2 in the fall, percent N in *C. maculosa* was similar to that of spikemoss and shallow-rooted forbs, and were 1.56%, 1.59%, and 1.21% respectively. Although percent N in spikemoss and shallow-rooted forbs differed from each other on this site in the fall. Percent N was lower in the grasses than other groups, except deep-rooted forbs on site 2 in the fall. All functional groups, except spikemoss, declined in plant N concentration from the spring to fall on both sites.

Phosphorus. Tissue P concentration depended upon functional groups and season at both sites (site 1: $F_{6, 218}=35.6$, $p < 0.0001$; site 2: $F_{6, 218}=28.2$, $p < 0.0001$). Spring percent P was similar for the spikemoss and grasses at both sites (Table 4.6). These values were lower than other functional groups on both sites. In the spring, shallow- and deep-rooted forbs had a P concentration about 1.5 times the value of that for grasses and spikemoss at site 1. In the spring, shallow- and deep-rooted forbs had a similar percent P in their plant tissue at site 2, averaging 0.20%. In the summer, percent P in deep-rooted forbs decreased by one-half to a percent similar to grasses on both sites. Shallow-rooted forbs

had the highest summer value of percent P which differed from other groups on both sites. On both sites in the fall, *C. maculosa* percent P was similar to shallow-rooted forbs and spikemoss, averaging 0.10%. On site 2 in the fall, *C. maculosa* percent P was also similar to deep-rooted forbs. Fall tissue concentrations of the shallow- and deep-rooted forbs remained similar to each other, averaging 0.08% on both sites. On both sites in the fall, deep-rooted forbs were also similar in P percent to grasses, while they were lower than spikemoss. Except for spikemoss on site 2, all functional groups declined in P concentration from spring to fall at both sites.

Potassium. Plant percent K depended upon functional groups and season at both sites (site 1: $F_{6, 218}=10.9$, $p < 0.0001$; site 2: $F_{6, 218}=4.5$, $p=0.0002$), and followed the same pattern in functional groups for each season at both sites (Table 4.6). Spikemoss percent K differed from all other functional groups and had the lowest percent K on both sites, averaging 0.34%. Percent K was at least three times higher in grasses than spikemoss in the spring and summer, and 1.5 times higher in the fall. Percent K in grasses differed from all other groups in each season, except for *C. maculosa* in the fall. Shallow- and deep-rooted forbs had similar percent K during all seasons. These values were twice as high as percent K in grasses. In the fall on site 1, percent K in *C. maculosa* (1.39%) was similar to the percent K in shallow-rooted forbs, deep-rooted forbs, and grasses. On site 2, fall percent K in *C. maculosa* (1.74%) was similar to the percent K in shallow- and deep-rooted forbs. Potassium declined seasonally in plant tissue concentration, except in the spikemoss functional group which remained relatively constant.

Sulfur. Plant S tissue concentration depended on the interaction of functional group and season on both sites (site 1: $F_{3,147}=18.6$, $p < 0.0001$; site 2: $F_{3,147}=28.6$, $p < 0.0001$). Spring sulfur concentration was similar, and lowest, for spikemoss and grasses on both sites, averaging 0.14% (Table 4.6). On both sites, tissue percent S in shallow- and deep-rooted forbs was similar to each other and differed from the spikemoss and grass functional groups by a factor of two. For all functional groups, except spikemoss, the percent S decreased throughout the growing season. Grasses retained the lowest amount of tissue S in the fall. This value differed from all other groups. *Centaurea maculosa* had a similar percent S as spikemoss and shallow-rooted forbs on site 1. On site 2, fall S concentration of *C. maculosa* was similar to shallow-rooted forbs, deep-rooted forbs, and spikemoss.

Plant nutrient uptake. **Site 1.** Plant nutrient uptake (concentration x plant biomass per meter square) depended on functional group and season for N, K, and S uptake (Table 4.7). For functional groups, means in the text and tables were averaged over seasons, while means for season were averaged over functional groups. Grasses, shallow-rooted forbs and *C. maculosa* had similar N and S uptake rates that differed from those of deep-rooted forbs on this site (Table 4.8). Nitrogen uptake by deep-rooted forbs was greater than the other groups by roughly 400 mg m⁻². Sulfur uptake by deep-rooted forbs was about twice that of shallow-rooted forbs and grass, and three times the amount of *C. maculosa*. Deep-rooted forbs had a higher K uptake on site 1 (1,000 mg m⁻²) than any other functional group. Shallow-rooted forbs K uptake also differed from all other

Table 4.7. *P*-values generated from ANOVA for nutrient uptake (concentration x plant biomass) by functional groups at sites 1 and 2. The error degrees of freedom for each site is 159 for N, P, K and 108 for S.

Site	Source	df	Nitrogen [†]		Phosphorus [†]		Potassium [§]		Sulfur [†]	
			F	P-value	F	P-value	F	P-value	F	P-value
1	Functional Group	3	11.46	<0.0001	11.05	<0.0001	22.59	<0.0001	9.24	<0.0001
	Season	2*	4.68	0.011	2.31	0.103	3.24	0.042	4.20	0.043
	Functional Group*Season	4	1.81	0.131	3.25	0.014	1.39	0.240	1.39	0.255
2	Functional Group	3	22.26	<0.0001	14.72	<0.0001	15.62	<0.0001	11.66	<0.0001
	Season	2	4.31	0.015	1.27	0.284	3.31	0.039	2.28	0.108
	Functional Group*Season	4	1.15	0.336	1.00	0.407	3.12	0.017	3.34	0.040

[†] The square root transformation was used for all ANOVAs except for sulfur on site 2. Non-transformed means are presented.

[§] Test results for the column represent the natural log transformation but non-transformed means are presented.

*df for sulfur is 1 for season and 2 for functional group*season because tissue samples were not analyzed for sulfur in the summer.

functional groups at site 1. At this site, K uptake was similar, and lowest, for grasses (258 mg m⁻²) and *C. maculosa* (186 mg m⁻²). Uptake of K, S, and C increased from the spring to the fall while N uptake remained the same. (Seasonal data not shown.)

Table 4.8. Significant differences in plant nutrient uptake among functional groups. A functional group's uptake values are the mean of spring, summer, and fall 2001 data. Values in each column which do not share the same letter are significantly different ($\alpha < 0.05$, ANOVA followed by Tukey post hoc test).

Functional Group	N ¹	Plant Nutrient Uptake (mg m ⁻²)				
		Site 1			Site 2	
		Nitrogen [‡]	Potassium [§]	Sulfur [‡]	Nitrogen [‡]	Phosphorus [‡]
Shallow Forbs	48	434a	492b	47a	315a	25a
Deep Forbs	48	787b	1000c	73b	659b	47b
Grass	60	352a	258a	31a	381a	26a
<i>C. maculosa</i>	4	242a	186a	22a	1468c	91c

[‡] Test results for the column represent the square root transformation, non-transformed means are presented.

[§] Test results for the column represent the natural log transformation, non-transformed means are presented.

¹ The N for Sulfur is grass: 40, shallow and deep-rooted forbs: 32 and *C. maculosa*: 4 due to samples in the spring and fall only.

Phosphorus uptake varied across seasons differently among functional groups at site 1 (Table 4.7). Site 1 spring P uptake was three times higher in deep-rooted forbs than in shallow-rooted forbs and grasses (Table 4.9). Phosphorus uptake by deep-rooted forbs decreased from the spring to summer giving all three functional groups similar P uptake values for the summer. In the fall, when *C. maculosa* was sampled, all functional groups had a similar P uptake, ranging from 17 to 43 mg m⁻². Uptake of P remained relatively constant for shallow-rooted forbs and grasses throughout the growing season at site 1.

Site 2. Plant nutrient uptake was affected by functional group and season for N and functional group only for P (Table 4.7). On this site, shallow-rooted forbs and grasses

had a lower N and P uptake than deep-rooted forbs and *C. maculosa* (Table 4.8). Deep-rooted forbs had a N uptake twice as high as the grass and shallow-rooted forb groups. *Centaurea maculosa* and deep-rooted forbs also differed from each other in N and P uptake. *Centaurea maculosa* had the highest N uptake on site 2 (1,468 mg m⁻²). *Centaurea maculosa* also had a higher P uptake than any other group. Total N uptake by plants was similar in the spring and fall, with a peak during the summer. (Seasonal data not shown.)

Table 4.9. Significant interaction results for plant nutrient uptake for functional group*season. Values in each column which do not share the same letter are significantly different ($P < 0.05$, ANOVA followed by Tukey post hoc test). P results are for site 1. K and S results are for site 2. For each functional group, the seasonal nutrient value is averaged over all removal treatments where the functional group was present. Seasonal variations of mean plant nutrient uptake within a functional group are presented in the text.

Functional Group	N	Plant Nutrient Uptake (mg m ⁻²)							
		Phosphorus [†]			Potassium [§]			Sulfur [†]	
		Spring	Summer	Fall	Spring [*]	Summer	Fall	Spring	Fall
Shallow Forbs	48	32a	47a	41a	276a	363a	376a	38a	34a
Deep Forbs	48	98b	52a	43a	483a	761b	912b	45a	76b
Grass	60	23a	30a	22a	255a	296a	217a	27a	31a
<i>C. maculosa</i>	4	n/a	n/a	17a	n/a	n/a	1653b	n/a	122b

[†]Test results for column represent the square root transformation but non-transformed means are presented.

[§] Test results for column represent the natural log transformation but non-transformed means are presented.

Nutrient uptake was affected by the interaction of functional group and season for K, and S on site 2 (Table 4.7). All functional groups had a similar K uptake in the spring, averaging 338 mg m⁻² (Table 4.9). In the summer and fall on site 2, grasses and shallow-rooted forbs had a similar K uptake while deep-rooted forbs K uptake differed and was greater. *Centaurea maculosa* K uptake was similar to deep-rooted forbs (1,653 and 912 mg m⁻², respectively) in the fall. Sulfur uptake did not differ among functional groups in

the spring on site 2. In the fall, deep-rooted forbs and *C. maculosa* had higher S uptake than shallow-rooted forbs and grasses. Potassium uptake by deep-rooted forbs increased throughout the growing season. Nutrient uptake remained seasonally constant for all other functional groups/nutrient combinations. (Seasonal data not shown.)

Effects of a nonindigenous invader on nutrient and hydrologic cycles

Soil contrasts. **Site 1.** Contrasts were used to test the hypothesis that the presence of *C. maculosa* would alter soil nutrient and water regimes. On site 1 in shallow soil depths, nitrate was greater, 2.5 versus 3.5 mg/kg, in the presence of *C. maculosa* where spikemoss was removed (Table 4.10). When all forbs were removed, shallow soil $\text{NH}_4\text{-N}$, P, and total C levels were higher in the presence of *C. maculosa* while soil water content was lower in the presence of *C. maculosa*. At site 1 in the shallow soil depth, S did not differ in the presence or absence of *C. maculosa*. (Data not shown.) At site 1 in deep soil depths, when all forbs were removed, soil water content was greater when *C. maculosa* was present (0.134 kg/kg versus 0.110 kg/kg) (Table 4.11). The presence of *C. maculosa* did not influence any other soil parameter, regardless of removal treatment, in site 1 deep soil depth.

Site 2. The presence of *C. maculosa* may have caused a decrease in soil $\text{NO}_3\text{-N}$, from 9.2 mg/kg to 8.3 mg/kg in the shallow soil depth and from 8.3 mg/kg to 8.0 mg/kg in the deep soil depth, where all vegetation was removed (Tables 4.12). Nitrate levels in shallow soil depths also were lower in plot with *C. maculosa* present when shallow-rooted forbs were removed. In shallow soil depths at site 2, soil $\text{NH}_4\text{-N}$ was nearly twice the

Table 4.10. MANCOVA contrasts to investigate the effect of *C. maculosa* on the mean soil parameters for site 1 shallow soil depth (0-15 cm). Removal treatment mean soil parameters were averaged over seasons. Removal treatments were initiated in the spring of 2000, and soil parameters measured spring, summer, and fall of 2001.

Treatments		Soil Nutrients and Other Soil Parameters									
Removal Treatment	<i>C. maculosa</i> Treatment	NO ₃ -N (mg/kg)	P-value §	NH ₄ -N (mg/kg)	P-value	P (mg/kg)	P-value	Total C (%)	P-value	Water content (kg/kg)	P-value
Control	absent	3.1	0.142	8.3	0.411	4.5	0.418	3.6	0.375	0.098	0.159
	present	3.4		8.4		4.0		3.7		0.088	
Spikemoss	absent	2.5	0.038	6.6	0.609	4.3	0.326	3.6	0.770	0.088	0.621
	present	3.5		7.8		5.8		3.8		0.091	
Shallow Forbs	absent	3.7	0.909	7.9	0.774	4.6	0.290	3.6	0.315	0.090	0.990
	present	3.9		7.1		4.0		3.6		0.091	
Deep Forbs	absent	3.3	0.175	7.7	0.444	4.0	0.880	3.3	0.323	0.099	0.952
	present	2.8		6.5		4.1		3.4		0.099	
Grass	absent	5.0	0.374	9.0	0.406	4.9	0.286	3.4	0.514	0.088	0.642
	present	3.3		6.5		3.9		3.6		0.091	
All Forbs	absent	4.2	0.644	8.5	0.013	4.7	0.055	3.4	0.053	0.098	0.018
	present	6.1		9.5		5.5		3.8		0.096	
All Plant Material	absent	10.9	0.497	10.7	0.779	6.4	0.787	3.7	0.935	0.097	0.380
	present	8.2		7.7		5.8		3.6		0.110	

§ Test results for the column represent the natural log transformation but non-transformed means are presented.

Table 4.11. MANCOVA contrasts to investigate the effect of *C. maculosa* on the mean soil parameters for site 1 deep soil depth (15-40 cm). Removal treatment mean soil parameters were averaged over seasons. Removal treatments were initiated in the spring of 2000, and soil parameters measured spring, summer, and fall of 2001.

Treatments		Soil Nutrients and Other Soil Parameters									
Removal Treatment	<i>C. maculosa</i> Treatment	NO ₃ -N (mg/kg)	P-value	NH ₄ -N (mg/kg)	P-value	P (mg/kg)	P-value	Total C (%)	P-value	Water content (kg/kg)	P-value ‡
Control	absent	3.2	0.441	8.5	0.784	3.8	0.618	2.7	0.811	0.109	0.672
	present	3.6		8.8		3.4		2.7		0.104	
Spikemoss	absent	4.0	0.566	8.3	0.818	3.5	0.860	2.7	0.908	0.095	0.888
	present	4.2		7.4		4.0		2.9		0.124	
Shallow Forbs	absent	6.3	0.467	11.3	0.510	4.1	0.811	2.7	0.565	0.096	0.449
	present	3.5		6.6		3.8		2.6		0.106	
Deep Forbs	absent	3.8	0.633	9.1	0.889	3.8	0.797	2.6	0.609	0.104	0.861
	present	4.2		8.2		3.7		2.7		0.109	
Grass	absent	4.5	0.617	8.7	0.776	4.3	0.237	2.9	0.243	0.108	0.892
	present	4.3		8.0		3.4		2.7		0.116	
All Forbs	absent	5.0	0.231	10.0	0.502	4.2	0.866	2.8	0.881	0.110	0.035
	present	5.7		8.1		4.4		3.0		0.134	
All Plant Material	absent	8.5	0.296	7.7	0.827	5.1	0.454	3.0	0.224	0.126	0.514
	present	7.9		12.1		4.4		2.5		0.108	

‡ Test results for the column represent the square root transformation but non-transformed means are presented.

Table 4.12. MANCOVA contrast to investigate the effect of *C. maculosa* on the mean soil parameters for site 2 shallow soil depth (0-15 cm) and deep soil depth (15-40 cm). Removal treatment mean soil parameters were averaged over seasons. Removal treatments were initiated in the spring of 2000, and soil parameters measured spring, summer, and fall of 2001.

Treatments		Soil Nutrients											
		Site 1						Site 2					
		NO ₃ -N (mg/kg)	P-value	NH ₄ -N (mg/kg)	P-value	Total C (%)	P-value	NO ₃ -N (mg/kg)	P-value	NH ₄ -N (mg/kg)	P-value	Total C (%)	P-value
Control	absent	1.5	0.559	5.7	0.687	3.5	0.431	2.1	0.178	5.1	0.348	2.5	0.196
	present	2.0		6.4		3.5		2.1		6.0		2.5	
Spikemoss	absent	2.1	0.492	5.9	0.785	3.4	0.703	1.8	0.623	5.7	0.108	2.3	0.101
	present	1.8		5.4		3.2		1.8		6.0		2.5	
Shallow Forbs	absent	2.7	0.457	7.1	0.509	3.4	0.939	2.5	0.002	5.9	0.830	2.4	0.980
	present	2.4		8.0		3.1		1.9		5.8		2.3	
Deep Forbs	absent	2.4	0.961	6.9	0.815	3.3	0.229	2.8	0.624	6.4	0.339	2.7	0.840
	present	2.3		6.7		3.6		2.4		7.0		2.3	
Grass	absent	3.2	0.332	7.8	0.575	3.3	0.170	2.5	0.189	6.3	0.621	2.7	0.113
	present	2.7		8.2		3.1		2.4		6.8		2.4	
All Forbs	absent	3.5	0.398	7.1	0.922	3.5	0.356	2.7	0.459	6.0	0.976	2.2	0.365
	present	3.2		7.9		3.5		3.1		6.8		2.8	
All Plant Material	absent	9.2	0.000	8.5	0.000	3.1	0.139	8.3	0.004	11.6	0.120	2.7	0.020
	present	8.3		15.5		3.3		8.1		13.8		2.5	

value in the presence of *C. maculosa* where all vegetation was removed. Total C levels in the site 2 deep soil strata was lower in the presence of *C. maculosa*. No differences were detected between the presence and absence of *C. maculosa* for total N, P, K, S, and soil water content for this site. (Data not shown.)

Plant tissue concentration contrasts. Plant tissue nutrient concentration (percent) was affected by the *C. maculosa* treatment in two cases on each site (Table 4.13). On site 1, percent S in deep-rooted forbs was lower when *C. maculosa* was present on the plots. Percent K in *C. maculosa* at site 1 was greater when *C. maculosa* was grown alone verses with other indigenous plants (0.19% verses 0.17%, respectively). On site 2, N and P concentrations were greater in *C. maculosa* when it was grown in the presence of other plants.

Plant nutrient uptake contrasts. ANOVA contrasts identified twelve differences in functional group nutrient uptake values between *C. maculosa* treatments (Table 4.14). On site 1, shallow-rooted forbs had roughly 1.5 times higher N, P, S, and C uptake when *C. maculosa* was absent. Sulfur and C uptake for the *C. maculosa* group were higher when *C. maculosa* was grown alone verses grown with other functional groups at site 1. On site 2, *C. maculosa* nutrient uptake was greater for all nutrients when *C. maculosa* was grown alone verses grown with other functional groups. In the absence of *C. maculosa*, deep-rooted forbs had a higher S uptake.

Table 4.13. ANCOVA contrast to investigate the effect of *C. maculosa* on mean plant tissue nutrient concentration (percent) of various functional groups. Means are the average of spring, summer, and fall 2001 values for each functional group. Covariant is the density of *C. maculosa* per plot.

Site	Functional Group	<i>C. maculosa</i> Treatment	Plant Tissue Nutrient Concentration (percent)							
			Nitrogen ¹	P	Phosphorus	P	Potassium	p [§]	Sulfur	p [§]
1	Spikemoss	absent	1.61	0.909	0.10	0.128	0.33	0.579	0.14	0.992
		present	1.59		0.11		0.32		0.13	
	Shallow Forbs	absent	1.67	0.209	0.15	0.788	1.88	0.121	0.22	0.332
		present	1.69		0.15		1.95		0.17	
	Deep Forbs	absent	1.92	0.998	0.15	0.938	2.03	0.362	0.19	0.027
		present	1.90		0.15		1.88		0.17	
	Grass	absent	1.34	0.898	0.10	0.115	0.99	0.473	0.12	0.531
		present	1.37		0.11		1.00		0.12	
	<i>C. maculosa</i>	alone	2.15	0.589	0.13	0.129	1.39	0.007	0.18	0.592
		with other plants	1.74		0.12		1.12		0.16	
2	Spikemoss	absent	1.53	0.857	0.09	0.609	0.36	0.893	0.14	0.712
		present	1.56		0.10		0.32		0.14	
	Shallow Forbs	absent	1.81	0.958	0.14	0.706	1.90	0.208	0.23	0.555
		present	1.80		0.15		1.95		0.17	
	Deep Forbs	absent	1.91	0.719	0.13	0.668	1.73	0.946	0.18	0.665
		present	1.85		0.14		1.66		0.17	
	Grass	absent	1.34	0.553	0.09	0.770	0.92	0.918	0.10	0.701
		present	1.32		0.10		1.00		0.10	
	<i>C. maculosa</i>	alone	1.56	0.023	0.10	0.049	1.74	0.211	0.13	0.109
		with other plants	1.88		0.11		0.95		0.16	

[§] Test results for the column represent the natural log transformation but non-transformed means are presented.

¹ The sample sizes vary due to differences in seasons sampled (S), the quantity of the tissue sample limited testing.

Table 4.14. ANCOVA contrasts to investigate the effect of *C. maculosa* on mean plant nutrient uptake (mg/m²) of various functional groups. Values are the means for spring, summer, and fall nutrient uptake for each functional group. Covariant is the density of *C. maculosa* per plot. Values for each functional group are significantly different at $\alpha < 0.05$. The natural log transformation was used for all ANCOVAs except for N, P, K, and S on site 2.

Site	Functional Group	<i>C. maculosa</i> Treatment	Plant Nutrient Uptake (mg m ⁻²)											
			N	n	P-value	P	n	P-value	K	n	P-value	S	n	P-value
1	Shallow Forbs	absent	434	60 ¹	0.012	40	60	0.006	492	60	0.092	47	40	0.032
		present	312	60		26	60		356	60		29	40	
	Deep Forbs	absent	787	48	0.493	64	48	0.575	999	48	0.912	73	32	0.374
		present	778	48		59	48		1000	48		61	32	
	Grass	absent	352	48	0.349	25	46	0.777	258	46	0.256	31	32	0.374
		present	315	48		24	47		232	47		27	32	
	<i>C. maculosa</i>	alone	243	4	0.174	17	4	0.864	186	4	0.133	22	4	0.018
		with other plants	27	9		4	2		35	2		2	9	
	Shallow Forbs	absent	315	60	0.468	25	60	0.462	338	60	0.745	36	40	0.251
		present	271	60		22	60		302	60		27	40	
2	Deep Forbs	absent	659	48	0.178	47	48	0.109	718	48	0.077	61	32	0.014
		present	590	48		42	48		580	48		55	32	
	Grass	absent	381	48	0.865	26	48	0.893	256	48	0.991	27	32	0.811
		present	399	48		32	48		298	48		31	32	
	<i>C. maculosa</i>	alone	1468	4	0.000	91	4	0.029	1653	4	0.001	122	4	0.000
		with other plants	31	12		7	3		81	3		2	12	

¹ The sample sizes vary due to differences in seasons sampled (S), the quantity of the tissue sample limited testing of all nutrients (P and K), and the limited amount of biomass present to sample (*C. maculosa*).

Discussion

Ecological role of indigenous functional groups and *C. maculosa*

Our data supported the hypothesis that indigenous functional groups have different ecological roles. Data also supported the hypothesis that removing functional groups would alter the nutrient and hydrologic cycles in soils because pools of N, P, and soil water were altered when one or more functional groups were removed (Vinton and Burke 1995, Dukes 2001, Peltzer and Kochy 2001). In our study, removing functional groups increased soil $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-H}$, P, and water. Therefore, functional groups may be using resources from different zones in the soil strata which are not accessible to other groups. The increase in unused resources in a functional groups absence implies functional groups may differ in resource capture, niche occupation and/or ecological role (Parriah and Bazzaz 1976, Berendse 1979, McKane et al. 1990, Golluscio and Sala 1993, Brown 1998, Carpinelli 2001). Similarly, Sala et al. (1989) found that resources freed by a functional group removal could only partially (or not at all) be used by another functional group. The increase in soil $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-H}$, P, and soil water could also reflect differences in a functional groups ability to fill unoccupied space (Symstad and Tilman 2001). Increased resource availability through functional group removals and/or seasonal variability could effect ecosystem processes such as competition intensity, and in turn, invasion (Burke and Grime 1996, Stohlgren 1999, Davis and Pelsor 2001, Dukes 2001, Herron et al. 2001). For example, if resource supply is unused, community invasibility may increase (Davis et al. 2000).

In some cases, differing ecological roles of functional groups were recognized when soil resources were lost in the absence of a particular functional group. Functional groups influence the input of resources to different soil strata via processes like penetration (Sala et al. 1989). For example, when all vegetation was removed, $\text{NO}_3\text{-N}$ increased in deep soil depths on both sites. This could reflect leaching of $\text{NO}_3\text{-N}$ from shallow to deep soil depths when the functional group diversity was lost and roots were not present to accumulate mineralized $\text{NO}_3\text{-N}$ in the upper soil profile (Symstad and Tilman 2001). Because functional groups respond differently to changes in community nutrient levels (Lauenroth and Dodd 1978, McLendon and Redente 1991, McJannet et al. 1995, Reich et al. 2001), altered nutrient availability due to the absence of a functional group could have affect community structure, nutrient cycling, and eventually ecosystem function. Soil parameters that increased in this study with or without the removal of a functional group may reflect soil heterogeneity more than functional group acquisition of resources.

Results of N, P, K, and S uptake by plants support the hypotheses that indigenous functional groups differ in ecological roles, and that removing one or more groups would alter the soil nutrient cycles (Pastor et al. 1984, van Breeman 1995, Vinton and Burke 1995). For most nutrients, the functional group with the greatest biomass had a greater uptake than other groups (Chapter 3). Removing this one group could have large implications on the community nutrient pools, and possibly on invasion.

Our plant nutrient results support the hypothesis that indigenous functional groups have different ecological roles because groups differed in N, P, K, and S concentrations

and uptake (Parriah and Bazzaz 1976, McJannet et al. 1995, Carrera et al. 2000, Duke and Caldwell 2001, Reich et al. 2001). Even functional groups within the same soil strata had different nutrient concentrations. This may indicate groups have different physiological demands from life history traits, ecological roles, and/or may be acquiring resources differently. Of all the functional groups, shallow- and deep-rooted forbs had the most overlap in which may reflect physiological demands of morphologically similar plants (Chapin 1993, Lambers et al. 1998) even though they occupy different areas of resource availability in the soil. Grasses overlapped in resource capture with the other groups, but its inconsistency in similarity of nutrient concentration with any one group suggests is more unique in ecological role than the other groups in the community.

Centaurea maculosa nutrient concentration was similar to all other functional groups on different occasions. However, nutrient concentration of *C. maculosa* tissue was usually similar to that of shallow-rooted forbs. Therefore, our data supports the hypothesis that indigenous and nonindigenous forbs have similar ecological roles (Johnson 1985, Thompson et al. 1995, Reich et al. 2001). This implies that the presence of one may exclude the other through resource preemption (Tilman et al. 1996, Symstad 2000, Davis and Pelsor 2001, Dukes 2001). Plant nutrient uptake data also supports this hypotheses because *C. maculosa* and indigenous deep-rooted forbs had similar values for nutrient uptake. These two groups have the greatest above and below ground biomass of any functional group and a higher resource acquisition may be required to meet demands for growth and reproduction (Tilman et al. 1999). *Centaurea maculosa* tended to have nutrient concentrations and uptake higher, singularly or with other groups, than other

functional groups. While indigenous groups and *C. maculosa* have similar ecological roles in this community, nutrient uptake and concentration rates that are as high or higher than indigenous functional groups could reflect the physiological demands of *C. maculosa*'s evolutionary environment. If *C. maculosa* evolved on nutrient poor soils, it may have the physiological ability to store and reutilize excess nutrients to increase its success of surviving (Lambers et al. 1998). If this is the case, then increased nutrient storage by *C. maculosa* could possibly decrease pools of soil nutrients in the invaded community over time if the rate of nutrient recycling differs from indigenous groups (van der Kift and Berendse 2001).

There was a degree of overlap in *C. maculosa* nutrient concentration with other groups. This may suggest indigenous and nonindigenous functional groups have similar ecological roles (Risser 1994, Vitousek 1990, LeJeune and Seastedt 2001), or that functional groups do not have complete niche differentiation (Bengtsson et al. 1994). Based on nutrient concentrations, we believe *C. maculosa* has a broad overlap in resource capture with other functional groups (Hoopes and Hall 2002). Plants may try to avoid competition through niche differentiation (Bengtsson et al. 1994) but all plants have similar resource demands and are drawing resources from the similar nutrient pools in soil strata which leads to overlap in nutrient consumption. For example, *C. maculosa* was similar to the spikemoss functional group nutrient concentration on some occasions possibly because they acquire resources from a similar soil nutrient pools. Ecologists have suggested that species with broad niche overlap may require disturbance for colonization

and that these plants may not be a superior competitors for resources but are more plastic to environmental changes such as alterations in resource availability (Bazzaz 1984).

This study supports the theory that maximizing niche occupation decreases the risk of invasion through preemption of resources by functionally similar indigenous and nonindigenous groups of plants. Diverse grassland communities may be more stable if a separation of resource use reduces the degree of competition among indigenous plants (Berendse 1979, Fowler 1986 and 1990). Ecosystem function can be maintained if the ecological role of an invader and an indigenous functional group are redundant (Schulze and Mooney 1993). Thus, preemption of resources by an indigenous group may exclude recruitment of a functionally similar nonindigenous group. Mechanisms and processes of competition exclusion are tied to resource fluctuations on spatial and temporal scales (Bengtsson et al. 1994). Because resource preemption can be affected by phenology, horizontal space, life stage, and/or rooting distribution (Parriah and Bazzaz 1976, Berendse 1983, Bengtsson et al. 1994, Fowler 1986, Hooper 1998), a plant community's risk of invasion can fluctuate over time and space as available soil nutrients may fluctuate by seasons and the presence of phenologically similar functional groups (Davis et al. 2000). Therefore, our results also consistent with the fluctuating resource theory of invasion. Spatiotemporal resource partitioning decreases the rate of competitive displacement among indigenous groups (McKane et al. 1990) while it might increase competition and decrease invasion among functionally similar invaders (Brown 1998, Carpinelli 2001, Dukes 2001). Invasive plant management that focuses on promoting

functional group diversity throughout the growing season should increase the likelihood that a functionally similar species will preempt resources and resist invasion (Chapter 3).

Nonindigenous invader effects on indigenous plant community

Research by D'Antonio and Vitousek (1992), Ehrenfeld et al. (2001), and Evans et al. (2001) indicates that nonindigenous invaders may effect soil nutrient. In this study, the presence of *C. maculosa* was correlated with soil nutrient levels on both sites, although the results were inconsistent. Invaders are thought to alter plant community nutrients to levels unsuitable to other vegetation. *C. maculosa* may impact nutrient cycles of a plant community by altering the degree of nutrient uptake by indigenous plants, the rate of decomposition (Christian and Wilson 1999, LeJeune and Seastedt 2001, Mack et al. 2001), and the frequency and intensity of disturbance regimes (D'Antonio and Vitousek 1992, Svejcar and Sheley 2001). We found soil parameter levels to be either higher or lower in the presence of *C. maculosa*, depending on parameter and/or soil depth.

Centaurea maculosa may be altering the soil parameter because all plots where a nutrient changed in the presence of *C. maculosa* had at least 16 *C. maculosa* plants m⁻². The two exceptions were where spikemoss was removed and NO₃-H was greater in the presence of *C. maculosa*, and where shallow-rooted forbs were removed and NO₃-H was lower in the presence of *C. maculosa*. Since 0.3-1.0 *C. maculosa* plants m⁻² existed on these treatments, we attributed these changes to natural soil heterogeneity. (See Chapter 3 for density data.) Our soil contrasts may be variable in this study because *C. maculosa* has only been present for 1 year and is still in the development stage. For example, *C.*

maculosa may be decreasing soil water in the shallow soil depth because it is a seedling (Sperber 2001). The increase in deep soil water on the same site and treatment may have occurred because deep-rooted forbs were removed in the treatment and *C. maculosa* roots had not matured to reach water in the deep soil depth. More time may be required for changes in nutrient and water cycles to become evident. It is also possible that the invader had no consistent impact on the indigenous community but rather adapted to conditions on the site (Svejcar and Sheley 2001). *Centaurea maculosa* may be similar enough to indigenous functional groups that it will never alter soil parameters, or changes will be difficult to detect (Mack et al. 2001). The lack of site-to-site similarities in soil nutrient alterations in the presence or absence of *C. maculosa* makes us reluctant to draw conclusion on these findings. We do not support or reject our hypothesis that a nonindigenous invader would alter soil nutrient and water cycles.

Nutrient concentration in plant tissue was altered in the presence of the invader (Ehrenfeld et al. 2001). Therefore, we support the hypothesis that the presence of a nonindigenous invader alters an indigenous functional group's ability to capture resources. There were significant differences in plant tissue nutrient concentration of *C. maculosa* grown alone versus *C. maculosa* grown with other plants. Nitrogen and P concentration was greater in *C. maculosa* when it was grown with other plants on site 2 implying *C. maculosa* may have a greater ability to compete for N and P (Blicker 2001, LeJeune and Seastedt 2001), or *C. maculosa* may be a stronger interspecific than intraspecific competitor for resources. Even though the nonindigenous invader was similar in nutrient concentration and content as indigenous functional groups, it may have competitive

mechanisms which are not present in the indigenous community that allow it to be a better competitor (Callaway and Aschehoug 2000). Therefore, the factors that allow a species to invade an area may be different than the factors allowing a species to dominate the community (LeJeune and Seastedt 2001). Changes in resource availability through the removal of key functional groups may have increased *C. maculosa* invasion success, but *C. maculosa* ability to compete for resources may allow it to persist and possibly dominate. While increased diversity may decrease invasion, it may not prevent the invader from being a successful competitor, altering ecosystem function, or decreasing community stability once it's established (Vitousek 1990, Evans et al. 2001).

Centaurea maculosa may be a better competitor for N and P than for K because percent K in *C. maculosa* was lower when it was grown in the presence of other vegetation. Being a better competitor for N and P compared to other soil nutrients may be advantageous for *C. maculosa* because these are commonly cited as limiting resources in semi-arid grasslands (Gleeson and Tilman 1990, DeLuca and Keeney 1994, LeJeune and Seastedt 2001). Sulfur concentration in deep-rooted forbs was lower in the presence of *C. maculosa* on site 1. It is possible that the juvenile and adult roles of *C. maculosa* differ and over time, *C. maculosa* may be more similar to deep-rooted forbs than shallow-rooted forbs in nutrient concentration. Our contrast results of plant nutrient concentrations in the presence and absence *C. maculosa* were not consistent between sites, perhaps because it was premature to detect alterations in the plant community from juvenile *C. maculosa* and/or the sample size may have been too small.

In support of our hypothesis, nutrient uptake by indigenous functional groups was altered in the presence of *C. maculosa*. Furthermore, the presence of indigenous forbs altered nutrient uptake of *C. maculosa*. Uptake of N, P, K, and S by *C. maculosa* was lower when it was grown in the presence of other vegetation versus when grown alone. Therefore, the presence of indigenous vegetation may be increasing competition and decreasing *C. maculosa*'s ability to acquire resources and produce biomass. On site 1, shallow-rooted forbs growing in presence of *C. maculosa* had lower N, P, and S uptake than shallow-rooted forbs growing in the absence of *C. maculosa*. The similarity in the plant tissue nutrient concentration of shallow-rooted forbs with *C. maculosa*, and our results of nutrient uptake contrasts, suggests these two functional groups compete directly for resources. As a key competitor with *C. maculosa*, the presence of the shallow-rooted forb functional group may be more important to invasion resistance than the presence of another group in large quantity. Similarly, Levine and D'Antonio (1999) suggested indigenous and nonindigenous species competing for resources is a likely explanation of invasion success. The presence or absence of a shallow-rooted forbs could completely alter plant community function and invasion resistance.

References

- AOSA. 2000. Rules for testing seeds Association of Official Seed Analysis, Lincoln, Nebraska.
- Bazzaz, F. A. 1984. Life History of Colonizing Plants: some Demographic, Genetic and Physiological Features. *In* Ecology of Biological Invasions in North America and Hawaii. H.A. Mooney and J.A. Drake (*eds.*) Springer-Verlag, New York, New York.
- Bengtsson, J., T. Fagerstrom, and H. Rydin. 1994. Competition and coexistence in plant communities. *Trends in Ecology and Evolution* 9(7): 246-250.
- Berendse, F. 1979. Competition between plant populations with different rooting depths. *Oecologia* 43: 19-26.
- Berendse, F. 1983. Interspecific competition and niche differentiation between *Plantago lanceolata* and *Anthoxanthum odoratum* in a natural hayfield. *Journal of Ecology* 71: 379-390.
- Blicker, P.S. 2000. Nitrate Uptake and Water Use of *Centaurea maculosa* (spotted knapweed) and native grasses. Thesis (M.S), Montana State University, Bozeman, Montana.
- Brady, N.C., and R.R. Weil. 1999. The Nature and Properties of Soil. Prentice Hall, Upper Saddle River, New Jersey.
- Bremner, J. M. 1996. Nitrogen-Total. *In* Soil Testing and Plant Analysis. SSSA Book Series: 3. R. Westerman (*ed.*) Soil Science Society of America, Madison, Wisconsin.
- Brown, C. S. 1998. Restoration of California Central Valley grasslands: applied and theoretical approaches to understanding interactions among prairie species. Thesis (Ph.D.) University of California, Davis, California.
- Burke, M. J., and J.P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* 77(3): 776-790.
- Callaway, R. M., and E. T. Aschehoug. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290: 521-523.

- Carpinelli, M. F. 2001. Designing weed-resistant plant communities by maximizing niche occupation and resource capture. Thesis (Ph.D.) Montana State University, Bozeman, Montana.
- Carrera, A. L., C. L. Sain, and M. B. Bertiller. 2000. Patterns of nitrogen conservation in shrubs and grasses in the Patagonian Monte, Argentina. *Plant and Soil* 224: 185-193.
- Chapin, F. S. I. 1993. Functional role of growth forms in ecosystem and global processes. *In: Scaling Physiological Processes: Leaf to Globe*. J.R Ehleringer and C.B. Field (eds.) Academic Press. San Diego, California.
- Christian, J. M., and S.D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the northern great plains. *Ecology* 80(7): 2397-2407.
- Clements, F. E. 1920. *Plant Indicators, the relation of plant communities to process and practice*. Carnegie Inst. Wash. Publ., Washington.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecological Systems* 23: 63-87.
- DeLuca, T. H., and D. R. Keeney. 1994. Soluble carbon and nitrogen pools of prairie and cultivated soils: seasonal variation. *Soil Science* 58:835-840.
- Daubenmire, R. 1970. *Steppe Vegetation of Washington*. Washington State University Cooperative Extension, Pullman, Washington.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528-534.
- Davis, M. A., and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. *Ecology Letters* 4: 421-428.
- Duke, S. E., and M. M. Caldwell. 2001. Nitrogen acquisition from different spatial distributions by six Great Basin plant species. *Western North American Naturalist* 61(1): 93-102.
- Dukes, J. 2001. Biodiversity and invasibility in grassland microcosms. *Oecologia*. 126: 563-568.
- Ehrenfeld, J., and Toth L. A. 1997. Restoration ecology and the ecosystem perspective. *Society for Ecological Restoration* 5(4): 307-317.

- Ehrenfeld, J. G., P. Kourtev, and W. Haug. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* 11(5): 1287-1300.
- Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. The University of Chicago Press, Chicago, Illinois.
- Evans, R. D., R. Rimer, L. Sperry, and J. Belnap. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications* 11(5): 1301-1310.
- Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. *Ann. Rev. Ecol. Syst.* 17: 89-110.
- Fowler, N. L. 1990. The effects of competition and environmental heterogeneity on three coexisting grasses. *Journal of Ecology* 78: 389-402.
- Gleeson, S. K., and D. Tilman. 1990. Allocation and the transient dynamics of succession on poor soils. *Ecology* 71(3): 1144-1155.
- Goelz, J. C. G. 2001. Systematic experimental designs for mixed species plantings. *Native Plants Journal* 2(1): 90-96.
- Golluscio, R. A., and O. E. Sala. 1993. Plant functional types and ecological strategies in Patagonian forbs. *Vegetation Science* 4: 839-846.
- Hamm, J. W., J. R. Bettany, and E. H. Halstead. 1973. A soil test for sulphur and interpretative criteria for Saskatchewan. *Communications in Soil Science and Plant Analysis* 4:219-231.
- Helmke, P. A., and D. L. Sparks. 1996. Lithium, sodium, potassium, rubidium, and cesium. p. 551-574. *In* *Soil Testing and Plant Analysis*. SSSA Book Series: 3. R. Westerman (ed.) Soil Science Society of America, Madison, Wisconsin.
- Herron, G. J., R. L. Sheley, B. D. Maxwell, and J. S. Jacobsen. 2001. Influence of nutrient availability on the interaction between spotted knapweed and bluebunch wheatgrass. *Society for Ecological Restoration* 9(3): 326-331.
- Hobbs, R. J., and L. Atkins 1988. Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australian wheatbelt. *Australian Journal of Ecology* 13: 171-179.
- Holechek, J. L., R. D. Peiper, and C. H. Herbel. 1989. *Range Management Principles and Practices*. Printice Hall, Englewood Cliffs, New Jersey.

- Hooper, D. U. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. *Ecology* 79(2): 704-719.
- Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Nature* 277: 1302-1305.
- Hoopes, M.F., and L.M. Hall. 2002. Edaphic factors and competition affect pattern formation and invasion in a California grassland. *Ecological Applications* 12(1): 24-39.
- Jacobs, J. S., and R. L. Sheley. 1998. Observation: life history of spotted knapweed. *Journal of Range Management* 51(6): 665-673.
- Johnson, H. B. 1985. Consequences of species introductions and removals on ecosystem function- implications for applied ecology. *In* Int. Symp. Biol. Contr. Weeds. E. S. Delfosse (ed.) Vancouver, British Columbia.
- Jones, J. B., Jr. 1977. Elemental analysis of soil extracts and plant tissue ash by plasma emission spectroscopy. *Communications in Soil Science and Plant Analysis* 8:349-365.
- Jones, J. B. and V. W. Case. 1990. Sampling, handling, and analyzing plant tissue samples. p. 389-427. *In*: Soil Testing and Plant Analysis. SSSA Book Series: 3. R. Westerman (ed.) Soil Science Society of America, Madison, WI. USA.
- Lacey, R. L., C. B. Marlow, and J. R. Lane. 1989. Influence of spotted knapweed (*Centaurea maculosa*) on surface runoff and sediment yield. *Weed Technology* 3: 627-631.
- Lambers, H., F. S. Chapin III, and T. L. Pons. 1998. *Plant Physiological Ecology*. Springer-Verlag, New York, New York.
- Lauenroth, W. K., J. L. Dodd, and P. L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia* 36: 211-222.
- Lavorel, S., A. H. Prieur-Richard, and K. Grigulis. 1999. Invasibility and diversity of plant communities: from patterns to processes. *Diversity and Distributions* 5: 41-49.
- LeJeune, K. D. and T. R. Seastedt. 2001. *Centaurea* species: the forb that won the west. *Conservation Biology* 15(6): 1568-1574.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of the evidence linking diversity and invasibility. *Oikos* 87: 15-26.

- Mack, M. C., C. M. D'Antonio, and R. E. Ley. 2001. Alteration of ecosystem nitrogen dynamic by exotic plants: a case study of C4 grasses in Hawaii. *Ecological Applications* 11(5): 1323-1335.
- Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13(5): 195-198.
- Maron, J. L. C., and Peter G. 1996. A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* 105: 302-312.
- McJannet, C. L., P. A. Keddy, and F. R. Pick. 1995. Nitrogen and phosphorus tissue concentrations in 41 wetland plants: a comparison across habitats and functional groups. *Functional Ecology* 9: 231-238.
- McKane, R. B., D. F. Grigal, and M. P. Russelle. 1990. Spatiotemporal differences in ^{15}N uptake and the organization of an old-field plant community. *Ecology* 71(3): 1126-1132.
- McLendon, T., and E. F. Redente. 1991. Nitrogen and phosphorus effects on secondary succession dynamics on a semi-arid sagebrush site. *Ecology* 72(6): 2016-2024.
- McNaughton, S. J. 1993. Biodiversity and function of grazing ecosystem. *In* Biodiversity and Ecosystem Function. E. D. Schulze, and H.A. Mooney (eds.), pp. 363-383. Springer-Verlag, New York, New York.
- Mueggler, W. F., and W. L. Stewart. 1980. Grassland and Shrubland Habitat Types of Western Montana. Intermountain Forest and Range Experimental Station, Ogden, Utah.
- Mulvaney, R. L. 1996. Nitrogen- Inorganic Forms. *In* Soil Testing and Plant Analysis. SSSA Book Series: 3. R. Westerman (ed.) Soil Science Society of America, Madison, Wisconsin.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. W. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734-737.
- Nelson, D. W., and L. E. Sommers. 1996. Total Carbon, Organic Carbon, and Organic Matter. *In* Soil Testing and Plant Analysis. SSSA Book Series: 3. R. Westerman (ed.) Soil Science Society of America, Madison, Wisconsin.

- Olson, B. E. 1999. Impacts of noxious weeds on ecological and economic systems. *In The Biology and Management of Noxious Rangeland Weeds*. R. L. Sheley and J. K. Petroff (eds.), pp. 4-18. Oregon State University Press, Corvallis, Oregon.
- Olsen, S. R., C. V. Cole, F. S. Watanabe, and L. A. Dean. 1954. Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate. USDA Circ. 939. USDA, Washington, DC.
- Orians, G. H. 1984. Site characteristics favoring invasion. *In Ecology of Biological Invasions in North America and Hawaii*. H. A. Mooney and J. A. Drake (eds.) Springer-Verlag, New York, New York.
- Parrish, J. A. D., and F. A. Bazzaz. 1976. Underground niche separation in successional plants. *Ecology* 57: 1281-1288.
- Pastor, J., J. D. Aber, C. A. McClaugherty, and J. M. Melillo. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* 65(1): 256-268.
- Peltzer, D. A., and M. Kochy. 2001. Competitive effects of grasses and woody plants in mixed-grass prairie. *Journal of Ecology* 89: 519-527.
- Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms and pathways of succession. *The Botanical Review* 53(3): 335-371.
- Prieur-Richard, A. H., and A. Lavorel. 2000. Invasions: the perspective of diverse plant communities. *Austral Ecology* 25: 1-7.
- Reich, P. B., D. Tilman, J. Craine, D. Ellsworth, M. G. Tjoelker, J. Knops, D. Wedin, S. Naeem, D. Bahaeddin, J. Goth, W. Bengtson, T. D. Lee. 2001. Do species and functional groups differ in acquisition and use of C, N, and water under varying atmospheric CO₂ and N availability regimes? A field test with 16 grassland species. *New Phytologist* 150(2): 435-448.
- Rejmanek, M. 1996. A theory of seed plant invasiveness: the first sketch. *Biological Conservation* 78: 171-181.
- Risser, P. 1994. Biodiversity and ecosystem function. *Conservation Biology* 9(4): 742-746.
- Robinson, G. R., J. F. Quinn, and M. L. Stanton. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* 76(3): 786-794.

- SAS Institute Inc. 1990. SAS/STAT Users Guide. Version 6, volume 2. Cary, North Carolina.
- SPSS Inc. 1999. Base 10.0 Users Guide. Chicago, Illinois.
- Sala, O. E., R. A. Golluscio, W. K. Lauenroth, and A. Soriano. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* 81: 501-505.
- Schulze, E. D., and H. A. Mooney. 1993. Ecosystem Function and Biodiversity. *In* Biodiversity and Ecosystem Function. E. D. Schulze, and H.A. Mooney (eds.), pp. 497-510. Springer-Verlag, New York, New York.
- Sheaffer, C. C., P. R. Peterson, M. H. Hall, and J. B. Stordahl. 1992. Drought effects on yield and quality of perennial grasses in the north central United States. *J. Prod. Agric.* 5(4): 556-561.
- Sheley, R. L., J. S. Jacobs, and M. F. Carpinelli. 1998. Distribution, biology, and management of diffuse knapweed (*Centaurea diffusa*) and spotted knapweed (*Centaurea maculosa*). *Weed Technology* 12: 353-362.
- Sheley, R. L., B.E. Olson, and L.L. Larson. 1997. Effect of weed seed rate and grass defoliation level on diffuse knapweed. *Range Management* 50(1): 39-43.
- Sheley, R. L., T. J. Svejcar, and B.D. Maxwell. 1996. A theoretical framework for developing successional weed management strategies on rangeland. *Weed Technology* 10: 766-773.
- Smith, M. D., and A. K. Knapp. 1999. Exotic plant species in a C₄-dominated grassland: invasibility, disturbance, and community structure. *Oecologia* 120: 605-612.
- Sperber, T. D. 2001. Soil Physical Properties and Soil Water Dynamics under Spotted Knapweed and Native Grasses. Thesis (M.S.), Montana State University, Bozeman, Montana.
- Stoddart, L. A., and A. D. Smith. 1943. *Range Management*. McGraw-Hill Book Co. Inc., New York, New York.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* 69(1): 25-46.
- Svejcar, T., and R. L. Sheley. 2001. Nitrogen dynamics in perennial- and annual-dominated arid rangeland. *Journal of Arid Environments* 47: 33-46.

- Symstad, A. J. 2000. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* 81(1): 99-109.
- Symstad, A. J., and D. Tilman. 2001. Diversity loss, recruitment limitation, and ecosystem functioning: lessons learned from a removal treatment. *Oikos* 92: 424-435.
- Thompson, K., J. G. Hodgson, and T. C. G. Rich. 1995. Native and alien invasive plants: more of the same? *Ecography* 18: 390-402.
- Tilman, D. 1988. *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, New Jersey.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379: 718-720.
- Tilman, D. 1997a. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78: 81-92.
- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie and E. Siemann. 1997b. The influence of functional diversity and composition on ecosystem process. *Science* 277(1): 1300-1305.
- Tilman, E. A., D. Tilman, M. J. Crawley, and A. E. Johnston. 1999. Biological weed control via nutrient competition: potassium limitation of dandelions. *Ecological Applications* 9(1): 103-111.
- van Beermen, N. 1995. Nutrient cycling strategies. *Plant and Soil* 168-169: 321-326.
- van der Krift, T.A. J., and F. Berendse. 2001. The effect of plant species on soil nitrogen mineralization. *Journal of Ecology* 89: 555-561.
- Vinton, M. A., and I. C. Burke. 1995. Interactions between individual plant species and soil nutrient status in shortgrass steppe. *Ecology* 76:1116-1133.
- Vitousek, P. M. 1984. *Biological invasions and ecosystem properties: can species make a difference? In Ecology of Biological Invasions in North America and Hawaii*. J. A. Mooney and J. A. Drake (eds.) Springer-Verlag, New York, New York.
- Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57: 7-13.
- White, L. M. 1973. Carbohydrate reserves of grasses: a review. *Journal of Range Management* 26(1): 13-18.

Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* 75(1):151-165.

Zar, J. H. 1999. *Biostatistical Analysis*, 4 edition. Prentice Hall, Upper Saddle River, New Jersey.

CHAPTER 5

SUMMARY

This research investigated ecological principles related to invasive plant management. The three overall objectives of this research were 1) to quantify the functional diversity of a grassland ecosystem, 2) to investigate the ability of functional groups (singularly or in combination) to resist invasion by a nonindigenous species, and 3) to quantify the ecological role of indigenous functional groups and a nonindigenous invader.

In Chapter 2, I hypothesized that the species and functional group diversity would be greater than previous descriptions for the *Festuca idahoensis*/*Agropyron spicatum* habitat type because a multiple-visits method would recognize seasonal and environmental variations in community composition. Of the species present, I hypothesized that forb functional groups account for the majority of the richness and biomass of a grassland plant community. Data supported the hypothesis that continuous, periodic sampling recognizes greater species diversity at one location because both sites were more diverse plant communities than previously described for this habitat type. I documented 14 graminoids and 69 forbs species from just two sites. Total diversity of a 4m² plot averaged 42 species, consisting of 5 grasses, 12 deep-rooted forbs, and 25 shallow-rooted forbs. My data also support the hypothesis that forb functional groups represent the majority of the richness and biomass of the grassland community. Forbs accounted for 83% of the species richness in this research.

In the invasion study in Chapter 3, I hypothesized that removing a functional group would yield higher densities and biomass of a nonindigenous invader, *Centaurea maculosa*, than that of the control, and that *C. maculosa* density and biomass would increase as functional groups were progressively removed. Furthermore, I also hypothesized that removing forb functional groups would increase *C. maculosa* biomass and density more than removing grasses because indigenous and nonindigenous forbs may share physiological and morphological traits and perhaps ecosystem function. Results were consistent with a growing body of evidence suggesting increased functional diversity decreases invasion. *Centaurea maculosa* density and biomass was higher at lower levels of functional group diversity on both sites. Data also supported the hypothesis that indigenous forbs would resist invasion by *C. maculosa* more than grasses because the absence of functionally similar groups was related to the higher *C. maculosa* densities and biomass. These results suggest the degree of functional diversity may not be as important in *C. maculosa* invasion as the functional composition of the community. My results indicated that indigenous forbs may compete more directly for resources with *C. maculosa* and their presence may be more important for invasion resistance than the presence of other functional groups.

To investigate the mechanisms behind invasion resistance, Chapter 4 qualified the nitrogen (N), phosphorus (P), potassium (K), sulfur (S), carbon (C), and water cycles in indigenous and nonindigenous functional groups. I hypothesized that indigenous functional groups have different ecological roles. I also hypothesized indigenous and nonindigenous forbs have similar ecological roles in cycling N, P, K, and S in plant tissue.

Data supported the hypothesis that indigenous functional groups have different ecological roles. Pools of soil resources increased in the absence of a functional group indicating that other groups were unable to obtain the unused resources. This implies functional groups may differ in niche occupation and ecological role. In support of the hypothesis that indigenous groups have different ecological roles, functional groups differed in N, P, K, and S concentrations and uptake. This may indicate groups have different physiological demands from life history traits, ecological roles, and/or may be acquiring resources from different niches. Data supported the hypothesis that indigenous and nonindigenous forbs have similar ecological roles because *C. maculosa* percent nutrient concentration was most similar to that of shallow-rooted forbs. Furthermore, *C. maculosa* and indigenous deep-rooted forbs had similar levels of nutrient uptake. This implies that the presence of one group may exclude the other through resource preemption. This study supports the theory that maximizing niche occupation decreases the risk of invasion through preemption of resources by functionally similar indigenous and nonindigenous groups of plants.

Because nonindigenous invaders are thought to impact ecosystem processes, I hypothesized in Chapter 4 that *C. maculosa* would alter nutrient and water cycles in the soil, and that the presence of *C. maculosa* would alter a indigenous functional groups ability to capture resources. In this study, the presence of *C. maculosa* altered soil nutrient levels on both sites, although the results were inconsistent. The lack of site to site similarities in soil nutrient alterations in the presence and absence of *C. maculosa* makes me reluctant to draw conclusion on these findings. I did not support or reject the

hypothesis that a nonindigenous invader would alter soil nutrient and water cycles. Plant nutrient data supported for this hypothesis that invaders alter the function of an indigenous group. Nutrient concentration and uptake in indigenous functional groups plant tissue was altered in the presence of the invader. Furthermore, N and P percent increased in *C. maculosa* when it was grown with other plants indicating *C. maculosa* may have a greater ability to compete for N and P than indigenous groups. The presence of indigenous forbs altered nutrient uptake of *C. maculosa*. Uptake of N, P, K, and S by *C. maculosa* decreased when it was grown in the presence of other vegetation versus when grown alone. Therefore, the presence of indigenous vegetation may be increasing competition and decreasing *C. maculosa*'s ability to acquire resources. Shallow-rooted forbs growing in presence of *C. maculosa* had lower N, P, and S uptake than shallow-rooted forbs growing in the absence of *C. maculosa*. The similarity in the plant tissue nutrient concentration of shallow-rooted forbs with *C. maculosa*, and results of nutrient uptake contrasts, suggests these two functional groups compete directly for resources. As a key competitor with *C. maculosa*, the presence of the shallow-rooted forb functional group may be more important to invasion resistance than the presence of another group in large quantity.

This study suggests that forbs are an important component to grassland community diversity, and establishing and maintaining a diversity of plant functional groups within the community enhances resistance to invasion. Indigenous forbs were particularly important to resisting invasion by nonindigenous forbs. Therefore, it is recommend that land managers recognize functional diversity, especially forb diversity, in grassland

management decisions. Indigenous forbs may be increasing resource competition and decreasing invasion success because they were functionally similar in percent tissue concentration and plant nutrient uptake to nonindigenous forbs. If indigenous forb functional groups that use resources similarly to nonindigenous forb invaders and are a critical component in community invasion resistance, then the goal of invasive plant management must be to establish and maintain these keystone functional groups.

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